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THE UNIVERSITY OF ALBERTA

A Systematic Revision of the North American Late Cretaceous Marsupial Genus *Alphadon* Simpson, 1927

by

Zerina Johanson

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF
Master of Science

Department of Geology

EDMONTON, ALBERTA
SPRING 1992

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Mark Wilson

Dr. M. V. H. Wilson

DATE: March 12, 1992

This thesis is dedicated to my father.

ABSTRACT

Alphadon Simpson, 1927 is a morphologically diverse North American marsupial genus ranging in age from the earliest Campanian to the latest Maastrichtian (late Cretaceous). Certain researchers have suggested that *Alphadon* is a grade taxon, and recently, *Alphadon* has been divided into three genera, including *Protalphadon* Cifelli, 1990a, *Turgidodon* Cifelli, 1990a and a restricted *Alphadon*. This thesis presents a revision of *Alphadon* (sensu lato) using the principles of phylogenetic analysis (cladistics).

Species assigned to *Alphadon* s.l. were evaluated, and taxonomic revisions were performed when necessary. Characters (based on the morphology of the dentition) were described and character states coded for the revised species of *Alphadon* s.l., as well as for four outgroup and four additional ingroup taxa. In all, 43 characters were coded for 21 taxa. These data were then analyzed with the PAUP 3.0 computer program. Thirty-six equal (minimal) length trees were found, and combined into a consensus cladogram which formed the basis for a new classification of *Alphadon* s.l. The results of the phylogenetic analysis support the separation of *Alphadon* s.l. into different taxa, including *Protalphadon* and *Turgidodon*, though the relationships of certain species to one another are not resolved. These uncertain relationships, in the form of polytomies, are represented in the classification through the use of the metataxon convention (the use of this convention is indicated by an asterisk following the metataxon name). In this classification, *Protalphadon* was found to be paraphyletic, but this paraphyly is resolved by removing "*Alphadon*" *creber* s.s. and "*Alphadon*" sp., cf. "*Alphadon*" *creber* from this taxon. These two taxa form a dichotomy, and are separated on the cladogram from *Protalphadon* and from a major polytomy including *Turgidodon*, *Alphadon marshi*, *Alphadon jasoni* and *Alphadon halleyi*. "*Alphadon*" *creber* s.s. and "*Alphadon*" sp., cf. "*Alphadon*" *creber* are assigned to the new metataxon, "new genus B*". *Turgidodon* is resolved on the consensus cladogram as a monophyletic taxon, but the relationships of this taxon to *Alphadon marshi*, *Alphadon jasoni* and *Alphadon halleyi* are unresolved. These four taxa are assigned to the higher-level metataxon, Alphadontinae*. *Alphadon marshi*, *Alphadon jasoni* and *Alphadon halleyi* are retained in *Alphadon* s.s., but because the relationships of these species to one another are unresolved, *Alphadon* s.s. is referred to as the metataxon *Alphadon* s.s.*

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DENTAL NOMENCLATURE AND MEASUREMENT

The terminology of the various morphological features (i.e., cusps, crests, basins) of the occlusal surface of both upper and lower molars referred to *Alphadon* and other marsupial taxa (**Figure 1**) are taken and modified from Bown and Kraus (1979) and Reig et al. (1987). Generally, upper molars will be indicated by a capital letter, i.e., M1, while lower molars will be indicated by a lower case letter, m1. In chapter 2, there is a short discussion of dental homologies, and upper and lower molars are indicated by the notation M1/1. This notation is part of the designation of dental formula; for example, in marsupials, the generalized dental formula is given as I5/4; C1/1; P3/3; M4/4. In this formula, I stands for incisors, C for canines and P for premolars. Measurements presented in this thesis are generally from upper molars, and less frequently from lower molars, and follow standard orientation of the teeth and direction of measurement (**Figure 2**), as provided by Clemens (1966) and Lillegraven (1969).

ABBREVIATIONS

Abbreviations for institutions in this thesis are as follows:

AMNH: American Museum of Natural History, New York
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge
MNA: Museum of Northern Arizona, Flagstaff
NMC: Canadian Museum of Nature, Ottawa
OMNH: Oklahoma Museum of Natural History, University of Oklahoma, Norman
SMNH: Saskatchewan Museum of Natural History, Regina
ROM: Royal Ontario Museum, Toronto
SMP-SMU: Shuler Museum of Paleontology, Southern Methodist University, Dallas
UALP: University of Arizona Laboratory of Paleontology, Tuscon
UALVP: University of Alberta, Laboratory for Vertebrate Paleontology, Edmonton
UCMP: University of California Museum of Paleontology, Berkeley
KU: Museum of Natural History, University of Kansas, Lawrence
UM : Museum of Zoology, University of Michigan, Ann Arbor

UNM-B: University of New Mexico, Albuquerque (U.S. Bureau of Land Mangement)

USNM: United States National Museum, Washington, D.C.

UW: Geological Museum, University of Wyoming, Laramie

YPM: Peabody Museum of Natural History, Yale University, New Haven

CHAPTER 1

HISTORY OF THE CLASSIFICATION OF THE NORTH AMERICAN LATE CRETACEOUS MARSUPIAL TAXON *ALPHADON* SIMPSON, 1927 (MARSUPIALIA)

The classification of the Late Cretaceous marsupial taxon *Alphadon* has changed dramatically since the genus was first erected by Simpson in 1927. Changes have occurred in the higher-level classification of *Alphadon* relative to other marsupial taxa and in the classification of various species within *Alphadon*. For example, species had been assigned to *Alphadon* with only some suggestion as to how these were related to one another. Recently, however, Cifelli (1990a) divided *Alphadon* into three genera, including a more restricted concept of *Alphadon*, which provided a better understanding of how referred species were related. With regards to higher level classification, *Alphadon* was originally classified with extant opossums (Family Didelphidae), but later removed from the Family Didelphidae and classified with other fossil marsupial taxa (Family Peradectidae (=Tribe Peradectini)). Marshall et al. (1990) erected a new cohort, Alphadelphia, to include certain primitive marsupial taxa, including *Alphadon*, and also to emphasize the distinctiveness of this genus and others from most other marsupial taxa. These authors also erected a new subfamily, Alphadontinae, to include *Alphadon* and a second Cretaceous (Early Campanian) taxon, *Albertatherium* Fox, 1971. Since the phylogenetic analysis presented in this thesis builds on earlier studies, and more particularly, on the recent studies discussed above, a thorough review of these is in order. This first chapter will discuss the history of these changes in the classification of *Alphadon*. This review will be chronological, and will begin after a short discussion of geographical and geological distribution of species assigned to *Alphadon*. Later chapters will deal with a discussion of the phylogenetic methods used in this analysis, taxonomic revisions of various species referred to *Alphadon*, and a final analysis, including the production of phylogenetic trees and a discussion of the resulting classifications. The use of the genus *Alphadon* in this chapter refers to *Alphadon* sensu lato, rather than the revised and restricted concept of *Alphadon* used by Cifelli (1990a), unless otherwise noted. **Figure 1** shows the various morphological features of a typical marsupial upper and lower molar that will be discussed throughout, and **Figure 2** depicts the standardized measurements and directions of measurement for these molars.

Alphadon marshi, the type species of *Alphadon*, was first described by Simpson in 1927. Simpson (1927) described this species on the basis of molar specimens from the

Lance Formation, Niobrara County, Wyoming, at one of the first North American Late Cretaceous mammal localities studied. This locality was first discovered by J. B. Hatcher in 1889 and extensively collected by field parties for O. C. Marsh between 1889 and 1892 (Simpson, 1929; Clemens, 1966). Since then, additional materials referable to *Alphadon* have been discovered at fossil localities across western North America. These specimens are recovered from geological formations of Campanian and Maastrichtian age (Late Cretaceous); there have been recent reports of specimens of Cenomanian age (earliest Late Cretaceous) from Utah (Eaton, 1990). The geographical distribution of Late Cretaceous localities producing materials of *Alphadon*, and the formations associated with these localities are given in **Figure 3**. In western Canada these formations include the Scollard (Lillegraven, 1969), Oldman and Milk River (Russell, 1952; Fox, 1971, 1976, 1979a, 1987a, b), and Ravenscrag and Frenchman formations (Johnston, 1980; Johnston and Fox, 1984; Fox, 1989; Storer, 1991).

Along with *Alphadon*, several other Late Cretaceous marsupial genera have been identified from the western North American fossil localities shown in **Figure 3**. These genera and their included species have been assigned to North American Late Cretaceous Land Mammal "Ages" or NALMAs. These "Ages" are characterized by the first, last and unique appearances of mammalian taxa (Lillegraven and McKenna, 1986; Archibald et al., 1987; Lindsay and Tedford, 1989), and were based on the mammal ages described for the Cenozoic of North America by the Wood Committee (Wood et al., 1941; Sloan, 1987). As various researchers have noted (Tedford, 1970; Lillegraven and McKenna, 1986; Lindsay and Tedford, 1989), these "Ages" differ from the standard definition of the Age unit given by the North American Code of Statigraphic Nomenclature (NACSN). As defined by the NACSN, an Age is a geochronologic unit corresponding to the time span of an established chronostratigraphic unit, so that the time span represented by the Age corresponds to the time span represented by the chronostratigraphic or rock unit (Lillegraven and McKenna, 1986). Each North American Land Mammal "Age" is considered to be a geochronologic unit, but with no necessary correlation of the boundaries (or time span) of the "Age" to the boundaries (or time span) represented by a corresponding chronostratigraphic (or rock) unit. This concept is different from that expressed by the original description of the NALMA given by the Wood Committee (Lillegraven and McKenna, 1986: 44-45), in that the boundaries of the "Age" unit were not necessarily exactly correlated to those of the type section, and were flexible, allowing for later modification. To express this, the term "Age" is placed in quotation marks (Tedford, 1970; Lillegraven and McKenna, 1986, based upon a suggestion by Savage, 1962).

Previous attempts to construct a series of Late Cretaceous NALMAs by Dorf (Lancian Age, 1942) and Russell (Paluxian, Aquilan, Judithian, Edmontonian and Lancian Ages, 1964, 1975) were criticized because these "Ages" were defined on the basis of chronostratigraphic units (as suggested by the NACSN), and did not follow the original intentions of the Wood Committee. Problems arose when fossil assemblages were considered to define and to be restricted to certain rock units. For example, Dorf established the Lancian Age on the basis of the Lance Formation in Niobrara County, Wyoming, and the "characteristic" mammal, dinosaur and plant fossils within. As Lillegraven and McKenna (1986) note, these fossils were used by Dorf to identify the Lancian Age, but do not define it. Russell (1975) correlated his Late Cretaceous "stages" with European (marine) stages, and considered the North American "stages" to be time rock units characterized by distinct faunas. Russell's "stages" were initially described on the basis of both vertebrate and invertebrate faunas, but increasingly became defined on the basis of better-known mammalian assemblages, as reviewed by Fox (1978). Nevertheless, the "stages" used by Russell were correlated to certain rock units, which corresponds to the definition of the stage unit given by the NASCN, but is not in keeping with the use of the Land Mammal "Age" of the Wood Committee (1941). Lillegraven and McKenna (1986) revised Russell's "stages", retaining the names, but characterizing them on the basis of species-level mammalian assemblages. For example, the Aquilan NALMA is based on the mammalian fauna from the upper member of the Milk River Formation, Alberta, the Judithian "Age" upon mammals from the Judith River Formation, Montana, and the Lancian "Age" on the fauna of the Lance Formation, Wyoming. The Edmontonian "Age" is not defined by Lillegraven and McKenna (1986) because of difficulties in recognizing a mammalian fauna characterizing this "Age". However, mammal faunas have begun to be recognized from the Edmontonian (R. C. Fox, pers. comm., 1990; Lillegraven and Ostresh, 1990); these include faunas from Kirtland and Fruitland formations, New Mexico (Lillegraven and Ostresh, 1990), as well as a new marsupial species, *Didelphodon coyi*, from the Horseshoe Canyon Formation, Alberta (Fox and Naylor, 1986), and a multituberculate, *Meniscoessus collomensis*, from the Williams Fork Formation of northwestern Colorado (Lillegraven, 1987).

Recently, Lillegraven and Ostresh (1990) have presented a preliminary correlation between the standard ammonite zonation for the Western North American Upper Cretaceous marine strata of Obradovich and Cobban (1975) and each NALMA. This work does not serve to define the NALMA as a true Age unit, since this requires some stratigraphic unit in which the fossils of the NALMA are found (not the Upper Cretaceous marine units), but provides an improved estimation of the duration of each NALMA in the Late Cretaceous. Though the definitions and uses of the Late Cretaceous NALMA have been widely discussed, there is little confusion among the researchers who use them to indicate the ages of various mammalian faunas and taxa. The Late Cretaceous NALMAs used most frequently in this thesis include (from oldest to youngest) the Aquilan, Judithian (with referred faunas from formations Campanian in age), and Lancian (Maastrichtian). The assignment of species discussed in this thesis to each of these NALMAs is shown in **Figure 4.** These species reflect the final classification reconstructed for this study and will not be discussed further here.

HISTORY OF CLASSIFICATION OF *ALPHADON*. The classification of *Alphadon*, until recently, has mostly been concerned with higher-level systematics, that is, with the relationships of *Alphadon* to other marsupial taxa. This classification has been and still is problematical. Part of this problem is due to the nature of the characters available for reconstructing these relationships. For Late Cretaceous marsupials, the bulk of the preserved fossil material consists of isolated teeth and less frequently jaw fragments preserving teeth in association. Species are recognized on the basis of characters observed from the premolars and molars, and particularly from the upper molars. This obviously limits the numbers and types of characters available to the taxonomist. Szalay (1982a, b) has criticized the use of dental characters in the classification of marsupial taxa because these characters are generally primitive or plesiomorphic for the marsupials as a whole. Szalay's criticism has merit, but still, dental characters are the only characters available, and more recent work suggests that marsupial taxa, including fossil taxa like *Alphadon*, can be identified on the basis of dental synapomorphies.

Beyond problems with the paucity of available characters, problems in classification arise because of homoplasy (convergence, parallelism and reversals) in these dental characters (Butler, 1972). Extensive homoplasy makes the choice of outgroups to the ingroup taxon being studied very difficult. Outgroups are used in this analysis to polarize character states (in a morphocline from plesiomorphic to derived) within *Alphadon*, the ingroup. Several taxa may share similarities with *Alphadon*, and thus be potential outgroups, but these similarities must be homologous, or having been present in a common ancestor shared with *Alphadon*. With fossil taxa, homoplasious and homologous character states are difficult to differentiate *a priori*, and this will be discussed further in Chapter 2. Of course, when outgroups are selected, the initial hypothesis is that these states are homologous, and homoplasious character states will be indicated after the cladogram has been constructed. Nevertheless, the initial hypothesis of homology between taxa is extremely important, and the abundance of homoplasy in dental characters increases the possibility that these initial hypotheses of outgroup relationship are incorrect. Homoplasy in dental character states is a major problem in this study, and implies that more time needs to be spent examining hypotheses of homology prior to the cladistic analysis. This approach has been suggested by Neff (1986) and Bryant (1989), and is followed here when possible.

The problems associated with "dental taxonomy" have plagued the studies of early mammals long before Simpson erected *Alphadon* in 1927. Additionally, researchers had to contend with faunas consisting of isolated teeth that had not previously been identified or classified in any mammalian taxon. The first North American Cretaceous mammals were discovered in Wyoming during the late 1800's, by field parties working for O. C. Marsh. Large numbers of specimens were discovered and Marsh (and later H. F. Osborn), attempted to identify and classify these as marsupials, placentals or multituberculates. Though *Alphadon* was not identified by Marsh or Osborn, the review of the classification of *Alphadon* presented here must begin with these studies, because Simpson (1927, 1929) later restudied the Wyoming faunas and revised the earlier classifications.

THE BEGINNING OF LATE CRETACEOUS MARSUPIAL CLASSIFICATION: O. C. MARSH, H. F. OSBORN AND G. G. SIMPSON. Simpson's first description of *Alphadon* and *A. marshi* in 1927, and a more comprehensive study in 1929, were based on a reexamination of the Late Cretaceous mammalian fauna collected from the Lance Formation (Maastrichtian), Niobrara County, Wyoming between 1889 and 1892. These mammalian materials were primarily isolated teeth (premolars and molars) and jaw fragments. This fauna was collected from windblown anthills common in the region, where the teeth and jaws had been accumulated through the action of insects (Simpson, 1929).

The original studies of this fauna by Marsh (1889a, b, 1891a, b, 1892), and Osborn (1891a-c, 1893) were only marginally successful in describing these materials and assigning them to different species and genera. Much of the fauna was referred to the Multituberculata (Marsh, 1889a, b, 1891a, b, 1892), and the rarer non-multituberculate material was referred to the Trituberculata. The Trituberculata comprised a poorly defined group consisting of taxa described from molars showing what Marsh and other early researchers believed was a trituberculate pattern, similar to molars referred to the Jurassic Trituberculata. Early researchers used the term "trituberculate" to describe a molar characterized by the possession of three cusps forming a triangle on the tooth, these three being a principal cusp on the inner side of the tooth called the protocone, and two smaller cusps positioned more antero- and posterior-external on either side of this principal cusp, the paracone and metacone (i.e. Osborn, 1887, 1888a, 1897, 1904; Cope, 1873, 1874, 1883a-c, 1884a; reviewed by Gregory, 1934 and Simpson, 1936). The names of these three cusps in the Jurassic forms were determined on the basis of an incorrect assumption of homology with the cusps of later mammalian upper molars. Today the term "trituberculate" refers to molars with three cusps in a triangular pattern, but the principal cusp previously designated as the "protocone" is now considered to be the paracone. Jurassic mammals (i.e. Eupantotheria) are properly referred to as trituberculates. The protocone is considered a neomorphic cusp not seen in the trituberculates, and molars that possess this cusp are termed **tribosphenic**, where the protocone of the upper molars occludes in a basined talonid (the term tribosphenic was first used by Simpson, 1936). The Late Cretaceous mammals described by Marsh and later Osborn as "trituberculate" are better described as tribosphenic, since these possess a true protocone and basined talonid, but the term "trituberculate" is retained for this part of the review, and placed in quotation marks to avoid confusion.

Because most of this "trituberculate" material studied by Marsh and Osborn was represented by isolated parts of the upper and lower dentitions, it was nearly impossible to decide whether these materials represented different parts of a single tooth row and should be associated in the dentition of one individual or whether they showed morphological differences that would allow them to be assigned to different species (this is still a problem for those who work on fossil mammals that are known primarily from teeth). Marsh took the extreme view, believing that it was necessary to describe, illustrate and name as much of this important material as possible, so he did, with little regard for whether these materials actually belonged to a single, individual dentition. Many of the "trituberculate" taxa named by Marsh were synonomized with other taxa by later workers, and Marsh himself eventually tried to revise some of these taxa, by referring different specimens to taxa on the basis that they represented different positions in the tooth row (Simpson, 1929: 98). This method was also problematic because of the lack of specimens preserving associated parts of the dentition. Two species named by Marsh that are still recognized today as belonging to the Marsupialia are *Pediomys elegans* and *Didelphodon vorax*. Marsh (1892) named several other taxa, and assigned these "trituberculates", including *P. elegans*, *D. vorax*, and the type Genus *Cimolestes*, to the Family Cimolestidae, and suggested that this family was related to modern opossums. Marsh believed that the "trituberculates" from the Lance Formation were marsupials but did note that some specimens may be referable to insectivoran taxa (also Matthew, 1916). Today, however, the Family Cimolestidae is not recognized as a valid family name and *Cimolestes* is considered to be a Late Cretaceous and Early Tertiary eutherian, assigned to the Family Palaeoryctidae (Kielan-Jaworowska et al., 1979).

Osborn (1891a-c, 1893) and Cope (1888, 1889), two of Marsh's contemporaries, criticized Marsh's taxonomic procedures, with most of these criticisms were directed to the large number of multituberculate taxa that Marsh had created. However, Osborn (1893) also recognized that for the "trituberculates", the referral of isolated upper and lower molars to an individual dentition or to a single species would be almost impossible, and that these problems could not be resolved until these molars were found in association. Osborn noted that as a temporary solution, descriptions of the Late Cretaceous "trituberculates" could be based upon **forms** or morphological types of upper and lower teeth alone, such that teeth grouped within species and genera were characterized by a particular morphology. Osborn (1893) recognized seven upper and five lower molar forms and considered that specimens assigned by Marsh to species of *Pediomys* and *Didelphodon* were similar to one or another of these molar forms, but did not attempt any revision beyond this. Osborn's methods seem to be an extreme reaction to Marsh's original methods of describing and naming species, and while Osborn certainly resolved some of the taxonomic confusion created by Marsh's original descriptions with regards to multituberculate taxa, he did not advance the classification of what are now recognized as Late Cretaceous marsupials beyond that established by Marsh for *P. elegans* and *D. vorax*. Nor did Matthew (1914, 1916), who supported Marsh's assertion that the "trituberculates" from the Lance fauna represented marsupials, but noted that there was no positive morphological evidence or evidence from dental formulae to suggest this (Matthew, 1916).

These early workers may not seem to have accomplished much in the way of identifying and classifying Late Cretaceous marsupials, but since there had been no previous studies involving descriptions of any Late Cretaceous marsupial taxa, researchers like Marsh and Osborn were truly pioneers. The recognition by Marsh that *Pediomys elegans* and *Didelphodon vorax* were in some way related to modern opossums was a major achievement, and provided the basis for later work by G. G. Simpson. Simpson (1927, 1929) reexamined Marsh's collections, and recognized the problematic nature of a revision of the taxonomy and systematic relationships of the Lancian fauna. After a brief paper (Simpson, 1927) providing redescriptions of several taxa, and descriptions of new taxa (i.e., *Alphadon* and *A. marshi*), Simpson (1929) attempted to provide a more complete classification of all the Lancian taxa, including the marsupials. He reviewed the methods of both Marsh and Osborn, and decided that both were questionable, but that Osborn's was preferable because it did not create a large number of poorly defined taxonomic names. Simpson (1927: 122, 1929: 99) recognized that his own genera, where established, must be "broadly drawn", with little or no attempt at a recognition of species beyond the type species. Therefore, Simpson did not assign the Lance specimens to a formal classification as such, but grouped these teeth according to their structure and morphology, much as Osborn (1893) had with his use of molar form.

Nevertheless, Simpson's higher level classification of the marsupial taxa from the Lance Formation goes beyond Marsh's assignment of these to the Family Cimolestidae. Simpson (1927, 1929) agreed with Marsh that the taxa that Marsh had assigned to the Family Cimolestidae were related to the modern opossums but instead used the Family Didelphiidae [sic], the family including modern opossums, for all primitive opossum-like fossils including Marsh's North American Cimolestidae, and the new Genus *Alphadon*. Within the Family Didelphiidae [sic], Simpson (1929) recognized four subfamilies (**Figure 5a**). These were the **Pediomyinae**, including *Pediomys* and *Nyssodon*, **Didelphodontinae**, including *Didelphodon*, *Alphadon*, *Ectoconodon*, *Thlaeodon*, *Stagodon*, and *Eodelphis*, **Microbiotheriinae**, including South American Tertiary marsupials; and **Didelphiinae** [sic], which included all living opossums and North American Tertiary marsupials. The description of the subfamily Didelphodontinae given by Simpson (1929: 116) was as follows-

> "Premolars bulbous, crushing. External cingulum [what is now called the stylar shelf] of molars uniformly broad, bilobed, nearly symmetrical, without marked metastylar or parastylar spur. Paracone and metacone subequal. Second style [now called stylar cusp B] large and heavy, others variable."

Simpson (1929, 1935) believed that the available Late Cretaceous specimens assigned to the subfamilies Pediomyinae and Didelphodontinae showed adequate morphological variation to be classified as separate families, but were too poorly known to be raised to this taxonomic rank.

Soon after Simpson's work, Hay (1930: 390), in a classification of the fossil vertebrates of North America, noted that Simpson's subfamily name Didelphodontinae had already been used by Matthew in 1918 for an insectivoran subfamily, so that Matthew's earlier use of this name had nomenclatural priority. Hay (1930) proposed a different subfamily name to replace Didelphodontinae, subfamily **Thlaeodontinae**, erected by Cope in 1892 as the Family Thlaeodontidae, based upon the type species *Thlaeodon padanicus*. *Thlaeodon* had been assigned to the subfamily Didelphodontinae by Simpson (1929), so that Hay (1930) applied Cope's family level designation, reducing it to subfamial rank in keeping with Simpson's original scheme of four subfamilies in the Family Didelphiidae [sic]. Besides *Thlaeodon*, *Alphadon*, *Ectoconodon*, and *Didelphodon* were classified in subfamily Thlaeodontinae, so that most of the genera assigned to Simpson's subfamily Didelphodontinae were retained in a single subfamily.

In 1935, Simpson acknowledged that the subfamily name Didelphodontinae Matthew, 1918 had nomenclatural priority over his usage for a subfamily of marsupials. Simpson (1935: 136) accepted Hay's designation of the Subfamily Thlaeodontinae, and provided a diagnosis of this subfamily that differed only slightly from that given for the Subfamily Didelphodontinae:

> "premolars crushing; upper molars with a broad, bilobed, nearly symmetrical stylar shelf; paracone and metacone subequal; no distinct metastylar spur; stylar cusp B large, heavy, other stylar cusps variable."

Other than this change from Subfamily Didelphodontinae to Subfamily Thlaeodontinae, Simpson retained the previous three marsupial subfamilies from his 1927 and 1929 classifications (**Figure 5b**), and emended the spelling of the family and subfamily ranks, Didelphiidae and Didelphiinae to Family Didelphidae and Subfamily Didelphinae. In 1945, Simpson compiled an extensive classification of living and fossil mammals, and in this he retained his earlier Late Cretaceous marsupial classification, including the Subfamily Thlaeodontinae.

This was where the state of classification of the Late Cretaceous marsupials, including *Alphadon*, stood until the late 1960's. Simpson (1927) described the Genus *Alphadon* and provided a higher level classification of the Late Cretaceous marsupials. Simpson (1929) had stressed though, that his revisions and newly described genera (including *Alphadon*) were broadly drawn, and based upon morphology and form. The newly described *Alphadon* was first classified in the Subfamily Didelphodontinae (Simpson, 1927, 1929), then in the Subfamily Thlaeodontinae (Hay, 1930; Simpson, 1935, 1945). All other Late Cretaceous marsupial genera were grouped at the subfamilial level as well, including the Subfamily Pediomyinae. Furthermore, these subfamilies were classified in the Family Didelphidae, that family including modern opossums.

W. A. CLEMENS. The next significant step in classification was provided by W. A. Clemens in 1966, based upon Late Cretaceous marsupials collected from the Lance Formation, Wyoming, from a rich new discovery in the Lance Creek Area at a site called Lull Quarry 2, among others (Clemens, 1963). Clemens's contribution to Late Cretaceous marsupial classification involved a major revision of Simpson's (1927, 1929, 1935, 1945) subfamilial classification. Clemens's (1966) classification was one of marsupial families, not subfamilies. For example, Clemens revised Simpson's Subfamily Pediomyinae, restricting it to the Genus *Pediomys* and raising the subfamily to family status, the Family **Pediomyidae.** More drastic revisions of Simpson's classification involved *Alphadon* and the Subfamily Thlaeodontinae. Clemens referred additional materials from the Lance Formation to *A. marshi*, and described two new species, *A. lulli* and *A. rhaister*. Clemens then removed *Alphadon* from the Subfamily Thlaeodontinae, and placed it in the Subfamily Didelphinae, Family Didelphidae. This revision was based on similarities between specimens referred to *Alphadon* and those referred to other taxa classified in the Family Didelphidae, as well as on a discovery by Patterson (1956) of isolated upper and lower mammalian teeth from the Trinity Sands (Albian), at the Greenwood Canyon locality, Texas. Molars from the Greenwood Canyon locality were considerably older than the earliest known marsupial or placental specimens (Early Campanian-Maastrichtian), but were similar to these in being tribosphenic, or possessing a protocone occluding in a basined talonid. Beyond this basic similarity, Patterson believed that there were no other available dental characters that would allow the Butler Farm materials to be confidently assigned to a marsupial or placental taxon. Instead, Patterson (1956) referred these former specimens to the "Theria of metatherian-eutherian grade", indicating that the Greenwood Canyon materials had reached an evolutionary grade similar to that of the placentals and marsupials (possession of tribosphenic molars) but were not assigned to either taxon. Patterson (1956) described these materials, but did not assign these to species or genera within the "therians of metatherian-eutherian grade".

Clemens (1966) considered the Early Cretaceous "therians of metatherian-eutherian grade" to be phylogenetically primitive, perhaps representative of the ancestral group from which marsupials and placentals arose. This assessment was based on a postulated ancestor-descendant relationship with the Jurassic eupantotheres (Patterson, 1956) and on their Early Cretaceous age relative to Late Cretaceous marsupial and placental taxa, such that the "therians of metatherian-eutherian grade" possessed an intermediate morphology between the non-tribosphenic eupantotheres and the tribosphenic but more morphologically derived marsupial and placental taxa. Clemens (1966, 1968) also noted that some upper molars assigned to this grade showed certain similarities to upper molars of *Alphadon marshi;* for example, both possessed a wide stylar shelf and large stylar cusps A and B, with cusp B being the largest on the stylar shelf. These similarities and others (large stylar cusp C; paracrista joining cusp B and paracone) were considered by Clemens to be primitive metatherian dental characters retained in *Alphadon*, so that *Alphadon* represented the most primitive marsupial taxon or the basal taxon in the metatherian radiation, and was ancestral to later marsupial groups. Differences between *Alphadon* and the "therians of metatherian-eutherian grade" included a relatively larger protocone and conules in *Alphadon* (Clemens, 1968).

Furthermore, Clemens (1966: 24) observed that four of the five dental characters given by Simpson (1935) to define the Subfamily Thlaeodontinae, 1) broad, bilobed, nearly symmetrical stylar shelves; 2) large stylar cusps; 3) subequal paracone and metacone and 4) lack of a distinct metastylar spur were molar features characteristic of a primitive grade of evolution for marsupials molars and retained in several lineages, including *Alphadon*. Since these characters were primitive, or more appropriately, plesiomorphic, they could not be used to define the Subfamily Thlaeodontinae. The character remaining from Simpson's diagnosis of this subfamily was large, crushing premolars. No premolars had been assigned to *Alphadon*, but the morphology of the alveoli for the premolars suggested that the crowns of these premolars were not large and crushing (Clemens, 1966). Therefore, Clemens removed *Alphadon* from the Subfamily Thlaeodontinae, and based upon the inferred ancestral-descendant relationship between *Alphadon* and Tertiary didelphid marsupials, referred *Alphadon* to the Subfamily **Didelphinae**, Family **Didelphidae (Figure 5c)**.

With regards to the remaining taxa classified in the Subfamily Thlaeodontinae, Clemens (1966) reviewed Marsh's (1889a, b, 1892) descriptions of what were then known to be Late Cretaceous marsupials and determined that *Ectoconodon* and *Thlaeodon* were synonyms of the third genus of this subfamily, *Didelphodon* Marsh 1889 (also Simpson, 1927). Also, Marsh (1889b) had described a type species, *Stagodon nitor* and established a family, Family **Stagodontidae**, to include this type species. Clemens redescribed *S. nitor* as a premolar of *Didelphodon*. Therefore, three of the subfamily or familial names established, Thlaeodontidae Cope, 1892, Thlaeodontinae Hay, 1930 and Stagodontidae

Marsh, 1889, were all based upon genera that Clemens considered to be synonyms of *Didelphodon*. The rules of systematic nomenclature require that the family level name chosen for this grouping be the one with priority, or the first name established for any of the genera that were eventually referred to *Didelphodon*. This would be the Family Stagodontidae Marsh 1889, which Clemens (1966) used to replace Subfamily Thlaeodontinae.

The extensive revisions and the new marsupial classification formulated by Clemens (1966) took an important step towards reducing the number of species names and taxonomic confusion associated with the Late Cretaceous marsupials. Also, by revising the higher level classification of these marsupials and raising the subfamilies of Simpson's classification (1929, 1935, 1945) to the familial level, Clemens emphasized the morphological and taxonomic distinctiveness of these taxa. Because of its stability, Clemens's classification of the Late Cretaceous marsupials was readily accepted by most researchers and soon became the standard classification. Later researchers using elements of Clemens's (1966) classification in their works include Ride (1964), Lillegraven (1969), Clemens (1968, 1971, 1979), Kirsch (1977), Clemens and Lillegraven (1986), Clemens and Marshall, (1976), Fox (1971, 1979a, b, 1987a, b, 1989), Sahni (1972), Marshall (1981), Montellano (1986, 1988), Johnston (1980), Johnston and Fox (1984), Archibald (1977, 1982), Lillegraven and McKenna (1986), Rigby and Wolberg (1987), and Flynn (1986).

Many of the advances in studies of *Alphadon* and other Late Cretaceous marsupials since Clemens's work involved discoveries of new Late Cretaceous faunas, rather than advances in classification. Several of these new faunas were older than those collected from the Lance Formation, and extended the range of *Alphadon* back to the Early Campanian. Some of these include faunas from the Judith River (Sahni, 1972; Montellano, 1986) and the Two Medicine formations (Montellano, 1988) of Montana, the Oldman Formation (Fox, 1979a) of Alberta, the "Mesaverde" Formation of Wyoming (Lillegraven and McKenna, 1986) and the Kaiparowits Formation of Utah (Cifelli, 1990a). These formations are all later Campanian in age, and the associated faunas are assigned to the Judithian NALMA. Fox (1971) described one of the earliest known faunas to produce a species of *Alphadon*, from the Milk River Formation (Early Campanian) of Alberta. *Alphadon creber* Fox, 1971 is assigned to the Aquilan NALMA. Cifelli (1990b) described materials from the Wahweap Formation of Utah, with these materials also assigned to the Aquilan.

Other Lancian faunas have also been described since Clemens's study, these serving to extend the geographical range of *Alphadon* across Western North America. In Canada, new faunas were described from the Scollard Formation of Alberta (Lillegraven, 1969), and from the Ravenscrag and Frenchman formations in Saskatchewan (Johnston, 1980; Johnston and Fox, 1984; Fox, 1989; Storer, 1991). Important specimens have been referred from the Hell Creek Formation (Archibald, 1977, 1982) of Montana. The stratigraphic relationships of these materials relative to the Cretaceous-Tertiary boundary have not been satisfactorily resolved. The most southerly extension of *Alphadon* is provided by faunas from the Fruitland and Kirtland formations of New Mexico. The "Age" assignment of these faunas is uncertain; some suggest that these are Judithian (Rigby and Wolberg, 1987), while others suggest they are "Edmontonian" (Lillegraven and Ostresh, 1990).

RECENT CHANGES IN CLASSIFICATION. The next major change in the classification of *Alphadon* did not occur until 1979, with work by J. -Y. Crochet. Crochet's studies (1979, 1980) involved a revision of the Subfamily Didelphinae (Family Didelphidae), the subfamily to which *Alphadon* had been assigned by Clemens (1966). The Family Didelphidae was considered to be a paraphyletic "wastebasket" taxon (Archer, 1984; Reig et al., 1985, 1987), where the term "wastebasket" implies that marsupial groups not possessing synapomorphies that would allow them to be grouped as monophyletic taxa or with other such taxa were "dumped" into the Family Didelphidae. Crochet's (1979, 1980) revision of the Subfamily Didelphinae partially rectified this situation by separating members of the subfamily into two tribes, and defining at least one the tribes, the **Tribe Didelphini,** on the basis of synapomorphic character states. The other tribe described by Crochet was the **Tribe Peradectini** (**Figure 5d**). The Didelphini included Tertiary marsupial taxa, as well as extant North American taxa. The Tribe Peradectini included *Alphadon* and four other marsupial genera, *Albertatherium* Fox, 1971, a taxon from the Milk River Formation, Alberta, *Bobbschaefferia* Paula Couto, 1970, a latest Cretaceous or Paleocene South American form, and two North American Paleocene genera, *Peradectes* Matthew and Granger, 1921 and *Mimoperadectes* Bown and Rose, 1979. The synapomorphies characterizing the Tribe Didelphini, as given in the diagnosis of the tribe by Crochet (1980: 58), are as follows:

> "Didelphinae à dilambdodontie de type didelphidien tendant rarement à atteindre un type talpedien; paracône plus bas que le métacône; face labiale de ces deux cuspides

formant un plan incliné; hypoconulide généralement plus bas que l'entoconide sur les trois premières molaires inférieures, et bien séparé de ce dernier par une échancrure."

Marsupial taxa that did not possess these characters states were classified in the Tribe Peradectini. The diagnosis of the Tribe Peradectini was therefore based on plesiomorphic molar character states (Krishtalka and Stucky, 1983b; Aplin and Archer, 1987; Reig et al., 1985, 1987; Cifelli, 1990a). The diagnosis for this tribe is as follows (Crochet, 1979, 1980: 38) -

> "Didelphinae prédilambdodontes, paracône et métacône sub-égaux et relativement coniques, hypoconulide et entoconide de hauteur voisine non seulement sur la M_4, mais sur toutes les molaires inférieures et reliès entre eux par une crête haute".

Dilambdodonty of the upper molars is considered an important morphological character in separating members of the Tribe Didelphini from the Tribe Peradectini (i.e., Marshall and de Muizon, 1988). Crochet (1979, 1980: 28) described his use of the term "dilambdodonty" as follows-

> "Une molaire supérieure de mammifère est de type dilambdodonte (le caractère correspondant étant la dilambdodontie) lorsque les paracrista, centrocrista et métacrista (c'est-á-dire l'éocrite de Vandebroek 1960-61) forme deux lambdas juxtaposés ou deux V renversés lorsque la dent est observée en vue occlusale en prenant pour base son bord labial."

Crochet focuses on the shape of the centrocrista in the three states of dilambdodonty that he describes, including **prédilambdodontie** (predilambdodonty, characteristic of members of the Tribe Peradectini), in which the centrocrista is straight or nearly so, **dilambdodontie didelphidienne** (didelphid dilambdodonty, Tribe Didelphini), where the centrocrista is V-shaped, with the apex of the V not reaching the labial edge of the molar crown, and **dilambdodontie talpedienne** (talpid dilambdodonty), where the V reaches the labial edge of the crown (Crochet, 1980: fig.4). Crochet's use of the term "dilambdodonty" has been recently criticized by Cifelli (1990a). Cifelli (1990a) noted that the term "dilambdodonty" properly refers to the entire ectoloph of the upper molars, including the centrocrista, the preparacrista and the postmetacrista, with these crests being strongly developed. Cifelli (1990a) suggests that Crochet's use of this term is incorrect, as Crochet appears to make reference to the centrocrista alone. The quote given above (Crochet, 1980: 28) indicates that this is clearly not the case. Other important characters separating the Peradectini and the Didelphini include the relative heights of the paracone and metacone, and various lower molar characters.

Crochet's classification was an important step forward because it revised the Subfamily Didelphinae by separating it into two tribes, of which the Didelphini at least could be defined as a monophyletic group, based on the synapomorphies given in the diagnosis. With regards to the classification of *Alphadon*, little was accomplished in that the Tribe Peradectini was still described on the basis of plesiomorphic character states, or on the basis of derived states (characterizing the Didelphini) that taxa assigned to the Peradectini did not possess. Further, taxa were classified in the Peradectini with little consideration of their phylogenetic relationships to one another. This included *Albertatherium*, which had been classified in the Family Didelphidae (along with *Alphadon*) by Fox (1971). On a cladogram, taxa classified in the Tribe Peradectini would be shown as an unresolved polytomy, and therefore, would be considered to be a metataxon (Gauthier et al., 1988a; = metaspecies, Donoghue, 1985). In a metataxon, there is no phylogenetic information provided by the available characters to resolve the relationships of the included groups to one another, or to taxa outside the group. The metataxon is given the "benefit of the doubt" (Donoghue, 1985: 178) and retained in phylogenies or classifications until more character evidence is found.

Other workers attempted to revise the classification of *Alphadon* and other Late Cretaceous and Early Tertiary marsupial taxa based on new evidence from other morphological systems. Szalay (1982a, b) based his classification of the Marsupialia on the morphology of the tarsal region rather than dental morphology. Szalay (1982a, 1982b: 182) made reasonable statements regarding problems involved in basing a taxonomy on dental character states, and believed that the Family Didelphidae, as defined by Clemens (1966) was a "broad and plesiomorphy-based use of the concept of Didelphidae...", because it was based primarily on dental characters. Using the morphology of the tarsus (including the astragalus and the calcaneum), Szalay determined that the living and late Cenozoic fossil taxa assigned to the Didelphidae possessed derived tarsal features, inherited from a common ancestor not shared by the Late Cretaceous marsupials assigned to the Family Didelphidae by Clemens (1966), including *Alphadon* and *Glasbius*. Thus, Szalay restricted the concept of the Didelphidae to taxa that possessed these derived tarsal characters and classified *Alphadon* and other Late Cretaceous taxa previously assigned to this family in an expanded Family Pediomyidae, based on the similarity of the dentitions of these taxa to what Szalay believed was the primitive dental pattern for the Marsupialia as a whole. The Family Pediomyidae now included the subfamilies Pediomyinae, Glasbiinae, Stagodontinae, and Peradectinae (including *Alphadon* and other species previously referred to the Tribe Peradectini).

Szalay acknowledged that the Family Pediomyidae was now a wastebasket taxon, and there is of course the problem of separating members of this family from the Family Didelphidae on the basis of tarsal morphology, when astragali and calcanei referable to *Alphadon* and members of the other subfamilies listed above have never been associated with known dentitions of these taxa. Szalay (1982a, b) noted that astragali and calcanei have been recovered from the Lance Formation and other formations of Tertiary age, and can be referred to the Pediomyidae (*sensu* Szalay) on the basis of the lack of derived morphological features observed on astragali and calcanei of the Didelphidae. Szalay's work had basically the same results as that of Crochet (1979, 1980)- the Didelphidae was reinterpreted as a monophyletic group on the basis of a derived tarsal morphology, resulting in the removal of *Alphadon* and *Glasbius* to the Peradectinae, and the inclusion of the Peradectinae and other Late Cretaceous subfamilies in the Pediomyidae, which lacked these tarsal synapomorphies. Szalay's use of the Family Pediomyidae has not been followed by subsequent researchers, and has been criticized by some (Fox, 1983), since it is used merely to lump Late Cretaceous taxa together, without accounting for the range of dental morphological diversity in the various referred subfamilies. As well, Szalay criticizes the use of dentitions in didelphid systematics because of the plesiomorphic nature of characters and character states involved, and he also questions the use of dental characters because only one morphological system is involved. However, Szalay's classification involves only one morphological system, the elements of the tarsus. Though Szalay's work shows that structures other than the dentition are available for use in marsupial systematics, it is far from complete (another researcher, J. R. Wible, has begun to study the morphology of what he suggests are Late Cretaceous marsupial petrosals from the Lance Formation (Wible, 1990, see also Archibald, 1979), comparing these to petrosals of better known marsupial taxa).

One important conclusion of Szalay's work was that the Marsupialia could be divided into the Cohort Ameridelphia, including North American (the Didelphidae and Pediomyidae, classified in the Suborder Didelphiformes) and South American forms (classified in the Suborder Borhyaeniformes), and the Cohort Australidelphia, including Australian taxa and the South American group, Microbiotheria. This division was again based upon differences in tarsal morphology, but is also supported by characters observed in extant taxa assigned to these cohorts, for example, sperm pairing in the Cohort Ameridelphia (Aplin and Archer, 1987). The division of Australian and North and South American marsupial taxa into separate cohorts has been incorporated into the studies of recent researchers (Aplin and Archer, 1987; Marshall et al., 1990), as have some of Szalay's tarsal characters. Lower-level classifications, for example, of the Didelphidae and Didelphinae, have followed Crochet (1979, 1980).

For example, Krishtalka and Stucky (1983 a, b) reexamined materials assigned to *Peradectes* and other North American Tertiary marsupial species, and provided revised diagnoses for the tribes Peradectini and Didelphini. These diagnoses (from Krishtalka and Stucky, 1983a, b) include the following-

> **Tribe Didelphini**: m1-3 with tall, spire-like entoconids; lower, posteriorly projecting hypoconulids, deeper, wider entoconid notches. M1-3 dilambdodont; paracone lower than metacone; strong conules and stylar cusps; posteriorly expanded protocone.

> **Tribe Peradectini**: m1-3 with low, subequal, and closely appressed entoconid and dorsally projecting hypoconulid; entoconid and hypoconulid separated by a weak entoconid notch and sharing a common internal talonid wall. M1-3 predilambdodont, paracone and metacone subequal, stylar cusps and conules weak, posterolingual part of protoconal base not expanded.

More importantly, Krishtalka and Stucky (1983b) removed *Alphadon* and *Albertatherium* from the Tribe Peradectini and restricted this tribe to *Peradectes*, *Mimoperadectes*, and a new genus from the Wind River Formation, Wyoming (Early Eocene), *Armintodelphys* Krishtalka and Stucky, 1983a. The removal of *Alphadon* and *Albertatherium* was based on the conclusion that certain members of the tribes Peradectini and the Didelphini possessed synapomorphies generally lacking in *Alphadon* and *Albertatherium*, including 1) lower molars with a shorter talonid relative to the trigonid and 2) a cristid obliqua that meets the posterior wall of the trigonid labial to the protocristid notch. On lower molars of *Alphadon* and *Albertatherium*, the cristid obliqua meets the posterior wall basal to the protocristid notch, and the talonid is longer than the trigonid. Therefore, Krishtalka and Stucky (1983b) believed that the Peradectini and Didelphini were sister taxa, sharing a common ancestry not including *Alphadon* and *Albertatherium* (also Montellano, 1988).

Furthermore, Krishtalka and Stucky (1983 a, b; also Clemens, 1984; Russell, 1984; Reig et al., 1987; Aplin and Archer, 1987; Cifelli, 1990a) noted that *Alphadon* may be a composite genus in that some derived character states of both the Peradectini and Didelphini variably occurred among the species assigned to *Alphadon*. For example, *A. marshi*, *A. rhaister*, *A. lulli* and *A. russelli* were said to have upper molars that show a certain degree of dilambdodonty, as in the Tribe Didelphini. Various upper molars from the Scollard Formation assigned to *A. marshi* (Lillegraven, 1969: fig. 15-3a) can be described as dilambdodont, and the taxonomic status of these will discussed in Chapter 3, in conjunction with a revision of *A. marshi* and *A. wilsoni*. Cifelli (1990a) noted that some upper molars assigned to *A. marshi* from the Scollard Formation possess a paracone that is lower than the metacone, similar to the state in the Tribe Didelphini, though a reexamination of the material does not support this observation. On these specimens, and similar well-preserved forms from the Frenchman Formation (Storer, 1991), the paracone and metacone are subequal in height. Most species assigned to *Alphadon* also have well defined stylar cusps and conules, as do members of the Didelphini. Krishtalka and Stucky (1983b) noted that *A. russelli* most closely resembled members of both tribes in having lower molars with shorter talonids, a more labial cristid obliqua, and resembled taxa assigned to the Tribe Peradectini in the possession of a closely appressed and subequal entoconid and hypoconulid and a weak entoconid notch (Krishtalka and Stucky, 1983b).

Krishtalka and Stucky (1983b) concluded that *Alphadon* could not be assigned to either the Peradectini or the Didelphini, but was instead a **grade** taxon, with some species possessing synapomorphies of both the Peradectini and the Didelphini, some possessing the synapomorphies of one or the other, and some species lacking the synapomorphies of either tribe. Since *Alphadon* had been considered by many researchers to be representative of the most primitive marsupial taxon (Clemens, 1966, 1968, 1977; Archer, 1976a; Kirsch, 1977; Fox, 1979, 1983; Szalay, 1982a, b), species were referred because they lacked dental synapomorphies seen in more derived marsupial taxa, with little consideration of the morphological variation involved (compare, for example, the morphology of *A. rhaister* with that of *A. creber* Fox, 1971 (**Figure 6A, B**)). The conclusion that *Alphadon* is a grade taxon would also suggest that *Alphadon* is "positively paraphyletic" (Donoghue, 1985), since evidence from various characters discussed above (Krishtalka and Stucky, 1983b) indicates that some species would be assigned to the Didelphini (i.e., *A. marshi* on the basis of dilambdodonty of the upper molars), and some would be assigned to the higher-level taxon (unnamed by Krishtalka and Stucky, 1983b) containing Peradectini and Didelphini (i.e., *A. russelli*). Since some species of *Alphadon* are more closely related to other taxa, *Alphadon* would not contain all descendants of the last common ancestor of this group, would be paraphyletic, and would have to be abandoned in a cladistic analysis. Krishtalka and Stucky (1983b) did not pursue this problem further in their study.

Archer (1984) also provided an alternative to Crochet's classification of the tribes Peradectini and Didelphini. Archer separated *Alphadon* from *Peradectes*, placing *Alphadon* and *Albertatherium* into a Superorder Alphadontia and *Peradectes* (as well as *Mimoperadectes* and *Bobbschaefferia*) into the Superorder Peradectadonta. Taxa classified in the Tribe Didelphini were assigned to the Superorder Didelphoidea. The Peradectadonta was separated from the Alphadontia on the basis of character states discussed in other works (Clemens, 1966, 1979; Crochet, 1980), and by the general reduction of stylar cusps in the Peradectadonta. Other North and South American taxa and Australian taxa were also classified at the Superorder level, and all were placed in the Cohort Metadelphia. Archer (1984) represented the relationships of the marsupial superorders as an eight branched polytomy. *Peradectes* was not more closely related to members of the Tribe Didelphini, as suggested by Krishtalka and Stucky (1983a, b), nor to *Alphadon*, as suggested by Crochet (1979, 1980). Archer noted (as had Crochet) that the character states given in the diagnosis of the Tribe Peradectini are diagnostic of the Marsupialia (or the Cohort Metadelphia) as a whole, and plesiomorphic at the level of the Tribe Peradectini. Therefore, these characters could not be used to define the Peradectini as a monophyletic group, and therefore it should be abandoned.

The revisions of Krishtalka and Stucky (1983) and Archer (1984) mark an important point in the classification of *Alphadon*, because both recognized that *Peradectes* and *Alphadon* do not share a close phylogenetic relationship, contrary to Crochet (1979, 1980). As well, Krishtalka and Stucky (1983) discussed the wide range of morphological variation in species referred to *Alphadon*, and Archer (1984) suggested that *Alphadon* was distinct from all other marsupial taxa by classifying *Alphadon* (along with *Albertatherium*) at the superorder level, equivalent to other marsupial superorders. However, the conclusions reached by Krishtalka and Stucky (1983) and Archer (1984) were generally ignored by the next researchers examining the higher-level relationships of the Marsupialia (Aplin and Archer, 1987) and the Suborder Didelphimorpha (Reig et al., 1985, 1987; Marshall, 1987).

These studies, most notably that of Reig et al. (1985, 1987) and Marshall (1987), claim to use cladistic analysis in that various characters are selected, character states are coded and the polarity of these states is determined through outgroup methods. The classifications derived are not strictly equivalent to the hypotheses of phylogenetic relationships produced by the analysis, as required in a cladistic analysis (Eldredge and Cracraft, 1980). These classifications include paraphyletic taxa and hypotheses of evolutionary distances between taxa, and are more characteristic of what are termed "evolutionary classifications" (i.e., Mayr, 1969; Eldredge and Cracraft, 1980). Marshall's (1987) study primarily concerned the relationships of South American marsupial taxa of Paleocene age, but his final classification did include *Alphadon* and other Late Cretaceous taxa, and is similar in most repects to the classification of Reig et al. (1985, 1987). These Late Cretaceous taxa were included in the analysis of Reig et al. (1985, 1987), which focused on the phylogenetic relationships of North and South American "opossum-like" marsupials, and included character evidence from serology, karyotypes, osteology (including the dentition) and reproductive anatomy. In a preliminary analysis, Reig et al. (1985: 335) recognized a "fundamental dichotomy of the opossum-like marsupials at the superfamily level", and separated these marsupials into the superfamilies Microbiotherioidea and Didelphoidea. The Microbiotherioidea included the families Microbiotheriidae, Caroloameghiniidae and Peradectidae (**Figure 5e**). *Alphadon* and *Peradectes* were classified together in the Family Peradectidae, with *Peradectes* being considered ancestral to the Didelphoidea, and the family as a whole ancestral to basically all other marsupial groups. Since *Peradectes* is said to be more closely related (ancestral) to the Didelphoidea, the Superfamily Microbiotherioidea does not contain all descendants of the last common ancestor of this taxon, and is paraphyletic. Though Reig et al. (1985, 1987) use a cladistic methodology, they retain this paraphyletic taxon in their classification, which is generally considered to be unacceptable by strict cladists. As well, these authors raised the Peradectini (Crochet, 1979, 1980) to the rank of Family (Reig et al., 1985, 1987: 75), noting that-

> "Provoked by Crochet's conclusion that *Alphadon* and *Peradectes* were closely related and constitute a separate group relative to other living and fossil didelphids... *Alphadon* and *Peradectes* closely approximate a hypothetical didelphomorph ancestor, having small differences which do not preclude their grouping, as proposed by Crochet (1980). We give full family status to this group, Peradectidae."

In a cladistic analysis, monophyletic clades are identified through the possession of shared derived characters, not through relative lack of differences, so that the ranking of a paraphyletic taxon (Tribe Peradectini) at the familial level on this basis is again, considered to be unacceptable. The Family Peradectidae has been subsequently criticized (Aplin and Archer, 1987; Cifelli, 1990a), but several researchers accept this family and its included genera, using it in their own classifications (also Marshall and de Muizon, 1988; Marshall et al., 1990; Cifelli, 1990a). The work of Reig et al. (1985, 1987) is important because of its extent and the large numbers of characters used from different morphological systems, and the level of resolution of the final phylogeny (actually a composite of several trees based on differing numbers of characters and taxa used; nevertheless, this composite shows better resolution than Archer's (1984) polytomy of the Metadelphia), but it did not advance the classification of *Alphadon*, and is in fact, a setback. By retaining the paraphyletic tribe Peradectini (Crochet, 1979, 1980), and giving this taxon family status, Reig et al. perpetuated the hypothesis that *Peradectes* and *Alphadon* lacked the synapomorphies of other more derived taxa, but yet were somehow related through the possession of shared plesiomorphic character states (symplesiomorphies), or as Reig et al. (1985, 1987) suggest, through the possession of small differences.

Aplin and Archer (1987: xx) describe their higher-level classification of the Marsupialia as "syncretic", in the sense that the classification is constructed from the best supported hypothesis of phylogeny, where no single character system has priority in phylogeny reconstruction if it is contradicted by other characters, and when there are contradictory results, the best supported hypothesis of relationships is chosen. This statement sounds like the application of unweighted parsimony methods, yet Aplin and Archer (1987: xxiii) clearly state that when this contradiction occurs, they use certain characters to resolve the conflict (i.e., basicranial morphology in preference to dental morphology), which is a form of character weighting. The weighting of certain characters in preference to others in a phylogenetic analysis is controversial, and is said to be unacceptable by some cladists (Eldredge and Cracraft, 1980; Schoch, 1986), since it is based on a subjective assessment of the value of certain characters in resolving relationships. One other problem involves the use of certain character systems that can not be recognized in all taxa being examined. Basicranial morphology may have a greater phylogenetic weight than dental morphology, but *Alphadon* and other Late Cretaceous marsupials are described predominantly on the basis of dental characters, so that a classification of the Marsupialia based preferentially on the basicranium is meaningless (at this point) for these Late Cretaceous taxa.

From their description of "mixed" or "polluted" classifications (Aplin and Archer, 1987: xxii-xxiii), as part cladistic and part something else (i.e., that of Reig et al., 1985, 1987), it could be assumed that the classification produced by Aplin and Archer follows directly from the results of their phylogenetic analysis (Aplin and Archer do not reproduce their character matrix or the final cladogram). However, these authors (1987: xxiv) describe a method they call "jacking up", where they evaluate the distinctiveness of various taxa in order to determine what Linnaean categorical rank to apply (subfamily, family, etc.). This is done after the cladogram is produced and relationships of taxa have been resolved. The methods used to evaluate distinctiveness of taxa include morphological and ecological distinctiveness, biochemical divergence and "antiquity", where antiquity is used in the sense that groups with a long geological history are more distinct than groups with a shorter geologic history. In other words, fossil groups are more distinct. Aplin and Archer (1987) deny that they have produced an "evolutionary systematist" classification (incorporating additional subjective information), and that their approach would have done so only if they had included estimates of taxonomic divergence **in the original** determination of phylogenetic relationship. Eldredge and Cracraft (1980) clearly state that in cladistics, hypotheses of relationship, as expressed in cladograms, have a one-to-one correspondence to relationships expressed in the resulting Linnaean classification- there is no point where additional information about the evolutionary history and divergence of taxa can be added to the final classification.

With regards to the status of *Alphadon*, Aplin and Archer (1987) retained the Family Peradectidae (**Figure 5f**), but assigned this family to "Marsupialia: cohort incertae sedis " along with other Late Cretaceous families, the Pediomyidae and Stagodontidae. These three families were designated "sedis mutabilis", a term used to indicate a polytomous or unresolved relationship among the three, and the classification in Cohort incertae sedis reflects the uncertainty regarding their relationships to other marsupial taxa. Aplin and Archer (1987: lxii) seriously question the status of the Family Peradectidae, and suggest that this taxon requires revision. These authors (1987: lxii) characterize the suggestion of Krishtalka and Stucky (1983b), that *Alphadon* and *Albertatherium* should be removed from the Peradectini (=Family Peradectidae), as "a more plausible scenario", yet still retain the Peradectidae, intact, in their classification.

The most recent studies reviewed here concern the classification of the Marsupialia as a whole (Marshall et al., 1990) and that of the various species assigned to *Alphadon* (Cifelli, 1990). Though Marshall et al. (1990) provide a revised classification for the Marsupialia as a whole, there is a significant portion devoted to the relationship of *Alphadon* to *Peradectes* and other marsupial taxa and to a revision of certain species referred to *Alphadon* (i.e., *A. creber*), with regards to the hypothesized ancestral marsupial morphotype. Marshall et al. (1990) present a cladogram showing the relationships of the Cohorts Ameridelphia, Australidelphia and a new cohort, Alphadelphia, to one another (**Figure 5g**). The Family Peradectidae is retained, and classified in the cohort Alphadelphia, but within the Peradectidae, *Alphadon* (and *Albertatherium*) are classified in the new Subfamily Alphadontinae, and separated from *Peradectes* and other taxa once assigned to the Peradectini, which are classified in the Subfamily Peradectinae. Taxa assigned to the Peradectinae are said to be derived relative to the members of the Subfamily Alphadontinae in a reduction of the conules and the stylar cusps (Marshall et al., 1990). Therefore, Marshall et al. (1990) have recognized the distinctness of *Peradectes* from *Alphadon* at the subfamily level, but still group these taxa together in the Family Peradectidae. The Subfamily Caroloameghiniinae is also classified in the Family Peradectidae.

Recent hypotheses regarding the morphology of the hypothetical marsupial morphotype have focused on upper molars and have suggested that stylar cusp C was lacking on these (Clemens, 1979; Fox, 1983, 1985, 1987a, b; Fox and Naylor, 1986; Clemens and Lillegraven, 1986). Two species referred to *Alphadon*, *A. creber* and *A. lulli* have been described as variably possessing stylar cusp C. Marshall et al. (1990) divided *A. creber* into two informal taxa on the basis of the presence (*A. creber* [+C]) or absence (*A. creber* [-C]) of cusp C. Because of similarities to the hypothetical ancestral marsupial in the absence of stylar cusp C and other morphological features (higher transverse width to anteroposterior length ratio for upper molars, greater trigon length, wide stylar shelf, closely appressed paracone and metacone, shorter protocone), *A. creber* [-C] was considered to represent the most primitive marsupial taxon, and to be basal to the Late Cretaceous radiation of marsupials. Marshall et al. (1990) classified *A. creber* [-C] in the Peradectoidea, incertae sedis, separate from *Alphadon* and other taxa within the Peradectidae. *A. creber* [+C] possessed most of the plesiomorphic marsupial character states as listed by Marshall et al. (1990) and observed for *A. creber* [-C], but possessed a stylar cusp C and a shorter trigon length (a ratio of the distance between the metacone and protocone to the anterior width of the tooth). *A. creber* [+C] was also removed from *Alphadon*, and classified within the Subfamily Peradectinae, even though *A. creber* [+C] was said by Marshall et al. (1990) to be an appropriate structural precursor for *Alphadon* (Subfamily Alphadontinae) as well as *Peradectes* (Subfamily Peradectinae). Problems with the classification of *Alphadon* presented by Marshall et al. (1990) are discussed later, in conjunction with a revision of *A. creber*. *Alphadon* and *Peradectes* were still considered to be closely related in this classification, and the paraphyletic taxon Peradectidae is retained. However, Marshall et al. (1990) take an important step in erecting two new taxa, the Subfamily Alphadontinae, and the Cohort Alphadelphia (to include the Family Peradectidae), equal in rank to the cohorts Austradelphia and Ameridelphia. Marshall et al. (1990; fig. 2) depict the relationships of the three cohorts to one another as a basal polytomy; no synapomorphies were found to suggest which two cohorts are most closely related to the exclusion of the third. Though Reig et al. (1985, 1987) were criticized earlier for raising the rank of the paraphyletic taxon Tribe Peradectini to that of family, the Cohort Alphadelphia recognizes the distinctness of its included taxa from members of the other two cohorts. The Cohort Alphadelphia and the Subfamily Alphadontinae will be discussed further in the final chapter of this thesis.

The last study discussed in this review of the history of classification of *Alphadon* is that of Cifelli (1990a), who noted that prior to his revision, North American Late Cretaceous marsupials lacking the derived character states of the pediomyids, the stagodontids, and of *Glasbius* were referred to *Alphadon*. *Alphadon*, therefore, was a "wastebasket " taxon, although all species classified in this genus did show a certain degree of morphological similarity. Cifelli (1990a) acted on suggestions that *Alphadon* s.l. was a composite taxon (Clemens, 1979: 214, 1984; Krishtalka and Stucky, 1983; Russell, 1984; Aplin and Archer, 1987; Cifelli and Eaton, 1987; Reig et al., 1987: 75), and divided *Alphadon* s.l. into three genera, including *Protalphadon*, and two more derived taxa, *Turgidodon* and a more restricted *Alphadon*. These taxa were classified in the Family Peradectidae. Three species were assigned to *Protalphadon*, "*A.*" *creber*, "*A.*" *lulli* and the newly described *P. wahweapensis* (Kaiparowits Formation, Utah, Campanian). Specimens assigned to *Protalphadon* were characterized by a smaller molar size, stylar cusp C variably present, wide stylar shelves, and an anteroposteriorly compressed protocone, among others. Most of these character states were included in the ancestral marsupial morphotype (and *A. creber* [-C]) by Marshall et al. (1990), but these authors suggested that this ancestor lacked stylar cusp C, and separated *A. creber* into two taxa on the basis of the presence or absence of this cusp. Cifelli's interpretation of the presence and absence of cusp C is that this cusp is variably present in taxa assigned to *Protalphadon*, including "*A.*" *creber* and "*A.*" *lulli*. These different interpretations will be examined later, as part of a revision of *A. creber* (Chapter 3) and *Protalphadon* (Chapter 5). For example, a consideration of the function or lack of function of stylar cusp C suggests that grouping specimens into taxa on the basis of the variable presence of cusp C is more plausible than splitting taxa on the basis of the presence or absence of this cusp.

Cifelli's study is important because it formally recognized the morphological diversity within *Alphadon* (sensu lato), through changes in classification of assigned species. The second genus named by Cifelli was *Turgidodon*, and species classified in this taxon include "*A.*" *russelli* Fox, 1979, "*A.*" *praesagus* Sahni, 1972, "*A.*" *rhaister*, and two new species from the Kaiparowits Formation, *T. lillegraveni* and *T. madseni*. Taxa assigned to *Turgidodon* are characterized by larger and more robust upper and lower molars, with strongly developed stylar cusps, especially cusp B, and by robust upper and lower premolars, with well developed wear surfaces on the apex of the paracone of P3. These character states are especially apparent on "*A.*" *praesagus* and "*A.*" *rhaister*. While Cifelli's use of *Turgidodon* seems justified, his use of the more restricted *Alphadon* does not. Here he describes new specimens from the Kaiparowits Formation referred to *A. halleyi* Sahni, 1972, *A. sahnii* Lillegraven and McKenna, 1986, and *A. attaragos* Lillegraven and McKenna, 1986, but does not provide a revised diagnosis or description for this newly restricted genus. Though not discussed, *Alphadon marshi* and *A. wilsoni* Lillegraven, 1969 would also be referred to *Alphadon* s.s, so that species that are not assigned to *Protalphadon* or *Turgidodon* are classified in *Alphadon* s.s. This is clearly unsatisfactory, since this *Alphadon* sensu stricto could be considered a "wastebasket taxon". However, Cifelli's work serves as a starting point for the analysis presented here, because an important step was taken in revising the relationships of the species once referred to *Alphadon*. There are many unanswered questions, and a great deal of revision still to be done. Some problems that must be resolved include the status of *Protalphadon* and the relationships of taxa classified in *Alphadon* s.s. by Cifelli (1990a). Other problems involve the relationships of all these taxa to *Peradectes* and the status of the Family Peradectidae. The work of Marshall et al. (1990) also provides a basis for further study, including the relationships of *Alphadon* s.l. to other marsupial taxa within the Subfamily Alphadontinae and the Cohort Alphadelphia, and to the cohorts Ameridelphia and Australidelphia.

CHAPTER 2-

METHODS OF PHYLOGENETIC ANALYSIS

CHARACTERS, CHARACTER STATES, HOMOLOGY AND OUTGROUPS. The principles of phylogenetic analysis have been discussed in many publications; thorough reviews are found in Wiley (1979), Eldredge and Cracraft (1980) and Schoch (1986), and these principles will be discussed only as they pertain to the particular analysis presented in this thesis. Phylogenetic analysis (cladistics) is concerned with monophyletic taxa, characterized by the possession of shared derived character states called synapomorphies. The first step in any phylogenetic analysis involves describing morphological characters and the character states associated with these characters. As used in this analysis, the definition of character is "a set of nested synapomorphies of character states" (Nelson and Platnick, 1981; Mickevich and Weller, 1990; Pogue and Mickevitch, 1990). This definition suggests the hierarchical nature of the distribution of character states on the cladogram (if there is no homoplasy involved) and that at some level of this hierarchy, all states will be synapomorphic (Eldredge and Cracraft, 1980; Patterson, 1982).

Since *Alphadon* is known only from isolated teeth and dentulous jaw fragments, the characters used in this cladistic analysis are all based on features of the occlusal surfaces of the upper and lower dentitions, primarily the upper molars. There are problems associated with using these types of characters, including the limited amount of information available from a single morphological system, the dentition, as compared to using additional information provided by skull and skeletal material. Second, characters of the dentition are susceptible to parallelism and convergence (Szalay, 1977, 1982a, b; Butler, 1978, 1982; Aplin and Archer, 1987), which is not surprising when one considers that the morphology of the occlusal surface (including cusps, crests and basins) is closely correlated with the feeding habits of the animal, which are often similar in unrelated taxa. The sabre-toothed cat, *Smilodon*, and the "sabre-toothed" marsupial *Thylacosmilus*, show a high degree of specialization for carnivory, including long, curved canines. These taxa are not closely related, but show similar adaptations for a particular feeding habit. Therefore, convergences should be recognized whenever possible and dismissed in favor of homology. Another problem involved with the use of dental characters is that since upper and lower molars form essentially a single functional unit, correlated or redundant characters may be coded separately from these molars. For example, in occlusion, the protocone of the upper molars fits into the talonid basin of the lowers, providing a crushing function to the dentition. Since the size of these two structures must be closely correlated in order to function in occlusion, should states for "size of talonid" and "size of protocone" be coded separately, or should only one state be coded?

These problems make it clear that the character analysis must be given special consideration. Some researchers (Szalay, 1982a; Neff, 1986; Bryant, 1990) have discussed the importance of character analysis in relation to phylogenetic analysis such that the cladogram is only a summary of the information already provided by the characters (Neff, 1986: 116), and cannot refute or support hypotheses of synapomorphy (or homology) because a most parsimonious cladogram only identifies incongruous characters that should be resolved through additional character analysis (Bryant, 1989). The suggestion that more emphasis should be placed on character analysis **prior** to the construction of the cladogram is strongly supported and functional and topological analyses of certain dental characters occur in this study. However, the role of the cladogram in refuting initial hypotheses of homology (and synapomorphy) is also strongly supported, especially for characters where other *a priori* analyses are inconclusive. With regards to the three problems mentioned above, there is little that can be done to improve the limited amount of information available in this analysis beyond finding new fossil localities and discovering cranial and postcranial materials of Late Cretaceous and Early Tertiary marsupials in association with known dental elements. The major problems to be solved in this analysis involve distinguishing between homoplasy (parallelism and convergence) and homology, and identifying redundant characters.

HOMOLOGY VS. HOMOPLASY. Homology is a central concept in phylogenetic analysis, and many definitions have been presented, with excellent reviews of these being provided by Wiley (1981) and Patterson (1982). An appropriate definition of homology is the following, "resemblance [similarity] due to inheritance from a common ancestor" (Simpson, 1961: 78). This implies that a feature present in two or more taxa was derived from the common ancestor of these taxa, and is recognized as such through similarity of this feature. Bock (1963) suggested that similarity should not be applied to the definition of homology, since the homologues need not be similar in the ancestor or even in the descendants as long as these homologues descended from a state present in the common ancestor (the homology between bones in the lower jaws of reptiles and the middle ear ossicles of mammals is a common example of this (i.e., Bock, 1963; Mayr, 1969: 85)). However, Bock (1977) later suggested that similarity is a test of homology, so that homology without similarity is untestable (Patterson, 1982: 24). Patterson (1982: 24) noted that one reason similarity has been rejected in definitions in homology is because of the circularity involved: similarity is used to infer homology and common ancestry, then this common ancestry is used to support the similarity as a homology. Nevertheless, it seems obvious that, especially in fossil studies where there may be no evidence available from ontogeny, homology between features in different taxa can only be postulated if some similarity is involved, at least initially. For this reason, Simpson's (1961) definition is the one used in this analysis.

Eldredge and Cracraft (1980: 36, 37; also Patterson, 1982 (and references within); Brady, 1985) relate homology to synapomorphy and symplesiomorphy, such that "synapomorphies are shared similarities (homologies) inherited from an immediate common ancestor; symplesiomorphies are shared similarities (homologies) inherited from ancestors more remote than the immediate common ancestor." This relates to the definition of "character" given above, that of a set of nested synapomorphies of character states (Nelson and Platnick, 1981; Mickevich and Weller, 1990; Pogue and Mickevitch, 1990), and the suggestion that all symplesiomorphies are synapomorphies at some level of the cladogram (Eldredge and Cracraft, 1980; Patterson, 1982). On the other hand, Duarte Rodrigues (1986) suggested that homology and synapomorphy are not equivalent terms; homology should be applied to "parts", or structures (Schoch, 1986), like stylar cusp C, rather than to the "attributes" or character states, like the presence or absence of cusp C. The term "synapomorphy" should instead be applied strictly to these "attributes". Researchers have used homology in both senses in marsupial systematics; Case (1988) discusses whether stylar cusp C is homologous or homoplasious among various marsupial taxa, pertaining to "parts" as suggested by Duarte Rodrigues (1986). Conversely, Cifelli (1990a) suggested that dilambdodonty (a character state associated with the shape of the centrocrista on the upper molars) was convergent in South American Paleocene marsupial taxa and in North American Late Cretaceous taxa. This example applies homology to the "attributes" or character states, and more specifically to synapomorphy, as suggested by Eldredge and Cracraft (1980).

For this analysis, homology will generally be equated with synapomorphy, and therefore with the "attributes" or character states rather than the "parts" or structures. A further example is given concerning the anteroposterior length of the talonid basin of the lower molars in two Tertiary marsupial taxa, *Peradectes* and *Peratherium*. Krishtalka and Stucky (1983b) suggested that a shorter talonid relative to the trigonid was a synapomorphy grouping these genera into a monophyletic taxon. A closer examination of the morphology of the lower molars of these two taxa suggest that this relatively shorter talonid basin is convergent. This does not suggest that the talonid basin itself is convergent in these two marsupial taxa, which would be the case if the concept of homology were applied strictly to "parts" (the talonid basin). Rather, convergence is recognized in the relative size of the talonid basin, referring to an "attribute" of the talonid basin. Though homology will be equated with synapomorphy in this analysis, there will be reference made to homology of structures, particularly in the consideration of outgroup taxa (i.e., is stylar cusp C homologous in *Holoclemensia* and the Marsupialia?). However, this use of the term homology still depends on a comparison of attributes of the structure or part among the taxa. For example, stylar cusp C may not be homologous in *Holoclemensia* and the Marsupialia because of differences in the size or shape of this cusp between the two taxa; stylar cusp D is considered to be homologous between the outgroups examined and the Marsupialia because of similarities in the position of this cusp on the stylar shelf in these taxa.

Since homology was defined as similarity due to inheritance from a common ancestor, a character state observed in two or more taxa is assumed, as an **initial hypothesis**, to have been present in or derived from a state in the common ancestor of these taxa. Therefore, similarity (in this character state) between taxa provides evidence for the initial hypothesis of homology (Cracraft, 1981), which may subsequently be refuted. Bock (1977) suggests that features in two or more taxa are homologous if they stem phylogenetically from the common ancestor of these taxa, and that similarity is a **test** of homology (or the “recognizing criterion” of homology, Eldredge and Cracraft, 1980: 35). If similarity is to be a test of homology, some criteria must be given for making the initial hypothesis of homology between taxa. It is difficult to deny, especially for fossil taxa, that an initial hypothesis of homology is based on similarity between taxa (Cracraft, 1981). This view is strongly endorsed in this analysis, so that other methods of testing initial hypotheses of homology must be used. Since homology has been related above to synapomorphy, one test of this initial hypothesis is through the congruency and convergence of character states on the cladogram (Gaffney, 1979; Eldredge and Cracraft, 1980; Patterson, 1982; Brady, 1985; Novacek, 1986a). After a cladogram has been constructed, certain character states will be congruent with one another, and define similar sets and subsets of monophyletic taxa on the cladogram. Other character states will not define these same sets of taxa and will be incongruent with the first states. These incongruent states are considered to be homoplasious, and would refute the initial hypotheses of homology of these states based on similarity between taxa. This use of incongruent character states to refute hypotheses of homology is a useful *a posteriori* method, but *a priori* methods may also be used. These would be used prior to the construction of the cladogram, and include the improved character analysis advocated by Neff (1986). Neff (1986: 116) criticizes the use of the *a posteriori* congruency method to refute hypotheses of homology, and suggests several *a priori* methods, including topological (in this analysis, including the relative positions of various cusps and crests to one another on the occlusal surface), and biomechanical (functional) relationships, among others.

Functional and topological relationships are considered in this analysis, but while functional relationships are used to test hypotheses of homology, topological relationships are used to suggest original hypotheses of homology (contrary to Neff, 1986). For example, a stylar cusp positioned labial to the paracone and connected to this cusp by a crest is called stylar cusp B, or the stylocone, and is considered to be homologous in all taxa in which these topological relationships occur (i.e., Patterson, 1956). A stylar cusp at or near the deepest part of the ectoflexus and between stylar cusps B and D on the labial edge of the stylar shelf is called stylar cusp C in taxa possessing it, and the presence of cusp C is initially considered to be homologous for these taxa. A consideration of functional relationships may be used to refute initial hypotheses of homology based on similarity in morphology and topological relationships, and specific examples are given below and later in this chapter. When considering functional relationships, an examination of the dentition is ideal because upper and lower molars are discrete functional units. During the chewing cycle, the lower molar moves past the upper so that elements of the lower are functionally correlated with elements of the upper (crests, cusps, basins), such that the size and morphology of these elements are closely related (Butler, 1961, 1972a; Vandebroek, 1961).

One example of the use of this methodology involves the position of the anterolingual portion of the cristid obliqua at the posterior wall of the trigonid (**Figure 1**) in certain marsupial taxa. On lower molars of "*Pediomys*" (said to be a composite taxon by Fox, 1987a, b), *Peradectes* and *Peratherium*, this portion of the cristid obliqua meets the posterior wall of the trigonid labial to the postcristid notch. This similarity allows for an initial hypothesis of homology between these three taxa. An examination of the functional relationship between the cristid obliqua and structures on the upper molars suggests that this may not be the case. As the lower molar moves against the upper during the chewing cycle, the cristid obliqua shears against the postparacrista (**Figure 7**), suggesting some sort of functional or topological relationship between these two crests, or even between the cristid obliqua and the paracone itself, since the postparacrista runs ventrobuccally from the apex of the paracone. Archer (1976b: 162-3) suggested that the position of the cristid obliqua (where it meets the posterior wall of the trigonid) reflected the position of the paracone, with a cristid obliqua that was buccal to the postcristid notch reflecting either a buccally placed paracone or a paracone that was reduced (in size, relative to the metacone). On upper molars of "*Pediomys*", the paracone and metacone are subequal in height, and the paracone is shifted buccally on the occlusal surface relative to the metacone. The paracone is reduced in size relative to the metacone in *Peratherium* and *Peradectes* (contrary to the suggestion of several authors, as discussed later in this chapter), but neither cusp is shifted buccally. The buccal position of the cristid obliqua can be correlated with the more buccally positioned paracone in "*Pediomys*", but with the reduced paracone in *Peradectes* and *Peratherium*. This consideration of functional and topographic relationships between the cristid obliqua and paracone strongly suggest that the similarity in the position of the cristid obliqua in *Peradectes* and *Peratherium* and in "*Pediomys*" is only an apparent similarity and is not homologous between "*Pediomys*"and these other two taxa. Most researchers (Clemens, 1979; Fox, 1979; Rigby and Wolberg, 1987) consider the buccal position of the cristid obliqua to be a synapomorphy for *Pediomys* s.l., rather than for a more inclusive group containing all three taxa, and Marshall et al. (1990) suggested that a more buccal position of the paracone was a synapomorphy for *Pediomys* s.l.

Cracraft (1981) denies that function can be used to refute hypotheses of homology since similarities between taxa need not be absolute to reflect homologous relationships. Cracraft (1981) suggests that the demand for a high degree of similarity would lead to some sort of "type" concept, and would deny the presence of morphological variation in these taxa. However, examples like the one given above for *Peradectes*, *Peratherium* and "*Pediomys*" do demonstrate that original hypotheses of homology can be refuted at the level of similarity prior to the phylogenetic analysis. One problem in using functional and topological relationships between upper and lower molars is in being able to recognize the full extent of these relationships. Perhaps they are more complex and involve relationships between more structural features than originally thought- would they extend eventually to the entire tooth? Fischer (1981) suggested that these types of functional relationships may extend to the entire organism. A satisfactory resolution to these problems may never be found, but it is important to recognize that they do occur. Functional and topological relationships, and their associated problems, are relevant to this discussion of redundant characters, discussed in the next section involving the coding and weighting of character states.

CHARACTER CODING. Character states used in the phylogenetic analysis discussed in Chapter 5 were coded 0, 1, 2, etc., and characters used in this analysis were both binomial (states 0 and 1), and multinomial (states 0, 1, 2...). A taxon-by-character data matrix was produced (**Chapter 4**), and this information entered in the computer program PAUP 3.0 for the MacIntosh (Swofford, 1987). The majority of the characters used were designated as unordered, where no order or direction of the character states was initially implied. Order indicates the organization of states in a transformation series or morphocline (0 1 2 3), without distinguishing the direction or polarity of these states, from plesiomorphic to apomorphic (0-1-2-3 or 3-2-1-0). Direction or polarity of the character states is determined through methods, such as outgroup analysis (Watrous and Wheeler, 1981; Maddison et al., 1984), which use taxa (the outgroups) most closely related to the group under study (the ingroup), such that character states found in outgroups and in the ingroup are plesiomorphic and cannot define monophyletic taxa within the ingroup. States found in the ingroup but not in the outgroup are apomorphic, and can define monophyletic taxa. Although the outgroup method can identify plesiomorphic and apomorphic (derived) states, it can neither order nor direct the derived states. This has led some authors to criticize the use of multistate characters, since the transformation series of these characters cannot be fully resolved. To overcome these problems, the use of alternative coding methods have been suggested, additive (Farris et al., 1970) and non-additive binary coding, that reduce the multistate character to binary characters. These approaches are not used here, and the order and direction of the character states used in this analysis were derived as discussed below.

After the characters states are entered in PAUP 3.0, the most parsimonious resolution of relationships among taxa is constructed, such that ad hoc hypotheses of homoplasy in these states are minimized. This simply suggests that a cladogram that requires three homoplasies in its reconstruction of relationships is preferable to a cladogram that requires more than three, other things being equal, and does **not** imply that evolution itself follows a most parsimonious course. Once this has been accomplished, the distribution of character states on the cladogram is indicative of the **order** of these states within the transformation series for each character. To determine the evolutionary direction or polarity, the cladogram is rooted by the program (PAUP 3.0 will attempt to root the cladogram such that the designated ingroup is monophyletic, if possible (Swofford, 1990)), and the transformation series can then be taken from the topology of this rooted cladogram, or from the distribution of terminal taxa and associated character states in this cladogram ("character phylogenies", Mickevitch, 1978; Mickevitch and Weller, 1990). One option in the PAUP 3.0 program charts the character state distribution for each character on the final cladogram(s), so that the polarity of these states can be read from this cladogram (**Figure 30**). In this way, the computer program resolves the transformation series for each character (via the distribution of states on the cladogram) without having to resort to binary coding.

Though the bulk of the characters used in this analysis were left unordered, two were entered as ordered. Generally, character states should be left unordered unless there is some evidence available for resolving the distribution of these states in the morphocline. This evidence can come from the sequence of the states in ontogeny, or through the fossil record. Maslin (1952; also Mickevitch and Weller, 1990) described a third methodology referred to as **morphocline analysis**, which is described as "a theory of character evolution that postulates a gradual shape transformation between states. In practice the amount of change is minimized over all states" (Mickevitch and Weller, 1990: 167). Here, character states are ordered such that morphologically intermediate states link morphologically extreme states (less derived and more derived). Unfortunately, mammalian molars are not replaced in the ontogeny of the animal, so there is no evidence available from different stages of tooth development. Evidence from the relative stratigraphic ages of taxa studied in this analysis, and from a consideration of intermediate states as some sort of "link" between morphologically extreme states will be used to order the character states for characters number 17 and 40 (**Chapter 4**). Character 17 is the "relative heights of paracone and metacone". For this character state, the states are numbered as "paracone larger and higher than metacone"-0; "paracone and metacone equal in height"-1; and "paracone reduced relative to the metacone"-2. State 0 occurs in the outgroup taxa (basal eutherians, Order Deltatheroida, *Pappotherium* Slaughter, 1968b), while state 1 occurs in *Alphadon* s.l., and state 2 in the more derived taxa (relative to *Alphadon* s.l.) included in the analysis (*Peratherium*, *Peradectes*, *Ankotarinja* and *Andinodelphys*). State 0 is the first state in the transformation series, being observed in the outgroup taxa, but the order of states 1 and 2 is uncertain (0-2-1 or 0-1-2?). Some rough evidence is provided by the relative ages of these taxa. The outgroup taxa are generally older, being Albian (*Pappotherium*), and ?upper Campanian in age (*Prokennalestes*, *Kennalestes*, the deltatheroidans, except *Sulestes*, Nessov, 1985, which is Santonian). *Alphadon* s.l. has a range from Early Campanian (*A. creber*) to latest Maastrichtian (*A. marshi*, among others), and the other more derived marsupial taxa are Tertiary in age. Using this information, the order of the states associated with the character "relative heights of paracone and metacone", would be suggested to be 0- 1- 2. However, *Alphadon lulli*, known from various Maastrichtian localities, possesses state 0.

Using the criteria given by Maslin (1952) above, that morphologically intermediate states should link morphologically extreme ones, and that the amount of change is minimized over all states (Mickevitch and Weller, 1990), the state "paracone and metacone equal in height" could be considered as morphologically intermediate between the two morphological extremes, the plesiomorphic state "paracone larger and higher than metacone", and what would be the other extreme, "paracone reduced relative to the metacone". The amount of change is also minimized in this tranformation series, involving a reduction in the paracone from states 0 through 1 to 2. These lines of evidence may seem weak, but increase in strength when considered together. Therefore, this character was initally ordered in this analysis. Character number 40, "position of the cristid obliqua at the posterior wall of the trigonid" is functionally correlated to the relative sizes of the paracone, as discussed later in this chapter. Briefly, the postparacrista (running posterolabially from tthe paracone) shears against the cristid obliqua as the lower molar shears against the upper. If the lengths of these crests are correlated, then a longer postparacrista would be related to a longer cristid obliqua. The postparacrista may increase in length if the paracone increases in height, and the cristid obliqua will increase in length if it meets the posterior wall of the trigonid in a more lingual position (at or near the metaconid). Taxa that have a larger paracone will generally have a cristid obliqua that meets the posterior wall of the trigonid more lingually (as in the outgroup taxa used in this analysis). The exception to this is *Alphadon lulli*, in which the paracone is larger than the metacone on the upper molars. Clemens (1966: 86-7, 1973: 88) referred certain lower molars to this species, and noted that the position of the cristid obliqua was positioned basal to the postcristid notch, as in other species of *Alphadon*. The reasons for this discrepancy may be 1) these lower molars are incorrectly referred to *A. lulli*; 2) the differences in height between the paracone and metacone on upper molars of *A. lulli* are not as great as on upper molars of the outgroup taxa 3) some other relationship between the paracone and lower molar structures is involved. Of these, the most likely seem to be 1) and 2). The relationship between the paracone and the cristid obliqua is readily recognizable.

Taxa having a subequal paracone and metacone (*Alphadon*) show a cristid obliqua positioned basal to the postcristid notch. Taxa whose upper molar show a paracone lower than the metacone (the ingroup taxa included) have a cristid obliqua that meets the posterior wall of the trigonid labial to the postcristid notch (nearer to the hypoconulid). Therefore, the relationship between the relative height of the paracone and the position of the cristid obliqua is generally consistent through the taxa in this analysis, and so, both characters should be ordered. Ordering character states adds information to the phylogenetic analysis by reconstructing the transformation series of certain characters, which will affect the distribution of the taxa (on the cladogram) characterized by states in this series. If these states were left unordered, their distribution on the cladogram would be affected by the most parsimonious distribution of other character states. Another method of adding information to the analysis is through character weighting, which suggests that some characters are more reliable in grouping monophyletic taxa than are others.

CHARACTER WEIGHTING. The weighting of certain characters implies that these characters are somehow more useful for resolving phylogenetic relationships than others. Character weighting can either be *a priori* (before the cladogram is constructed) or *a posteriori* (after the cladogram is found, and changes are required). As Wheeler (1986) has noted, all phylogenetic analyses contain some form of *a priori* character weighting, including the original choice of characters for use in the analysis, the specimens studied, and the methods of analysis. Wheeler (1986) also notes that not weighting characters *a priori*, the method prefered by most cladists, is in fact a subtle but entirely objective form of weighting in which all characters are originally given an equal weight.

In PAUP 3.0, different weights can be applied to characters *a priori*. This initial character weighting implies that the researcher has some *a priori* knowledge of the "importance" of certain characters. This type of *a priori* weighting of characters has been questioned by many researchers, including Eldredge and Cracraft (1980), who note that weighting is unnecessary because characters weight themselves through synapomorphy, and all character states are synapomorphies at some level of the cladogram (even if this level is beyond that of the basalmost outgroup). No *a priori* weighting methods were intentionally used in this analysis (unless one counts the ordering of the characters "relative heights of the paracone and metacone" and "position of the cristid obliqua at the posterior wall of the trigonid" as some form of weighting). PAUP 3.0 also has an option that allows for an *a posteriori* method of character weighting; this is the successive approximations method of Farris (1969). In this method, characters are reweighted relative to their amount or degree of homoplasy on the cladogram, and is used in this analysis because while similarity was used as an initial hypothesis of homology (equal to synapomorphy), the distribution of character states on the cladogram was said to be regarded as an *a posteriori* test of this hypothesis. The use of the successive approximations method follows from the results of this test.

Other forms of character weighting were not as obvious as that described above, but were still present. For example, weighting occurred in the application of *a priori* character analyses involving an examination of topological and functional relationships between different molar structures. As in the example above involving "*Pediomys*", *Peradectes* and *Peratherium*, initial hypotheses of homology were overturned by a consideration of these types of relationships. As well, further examination in the course of assembling the data set revealed characters that were considered to be "poorer" characters, including those that were difficult to consistently code among taxa, and those that were difficult to consistently recognize and code. These characters should perhaps not have been included in the first place, but their removal does effectively give them a weight of zero. This type of removal occurs in the development of any data set, but could still be criticized in that not all possible characters are being considered in the analysis. Another example of *a priori* weighting would involve the retention of redundant characters. If upper and lower molars are functional units (Butler, 1941, 1961; Lillegraven, 1969; Crompton, 1971), will characters coded from functionally related structures on the upper molars and lower molars represent essentially the same character? An example given earlier involved the protocone of the upper molars and the talonid basin of the lowers, such that the size of the talonid (both transverse width and anteroposterior length) is correlated with the size of the protocone (Archer, 1982b; Fox, 1975, 1983). An anteroposteriorly short protocone is considered to be a plesiomorphic state for the Marsupialia (Marshall et al., 1990: 437; Cifelli, 1990a), so that a lengthening of this protocone would be an apomorphic state within the Marsupialia. If the size of the talonid is correlated with the size of the protocone, one would expect that the longer protocone would be correlated with a longer talonid basin. Should the former be coded in a phylogenetic analysis, as well as the latter? In a sense, this would be coding for the same character twice, or coding redundant characters (Fischer, 1981; Schoch, 1986). This would be a form of character weighting, and more importantly, it is a form of weighting that the researcher cannot always recognize, and therefore has little control over. Since upper and lower molars are functional units, it would be expected that most morphological features on the uppers are related to features on the lowers, but these relationships may not always be observable, or the relationships may be more complex than originally thought.

A second example of coding redundant characters, already briefly mentioned earlier, involves relationships between paracone and metacone of the upper molars and the postcristid and cristid obliqua of the lowers. As the lower molar moves past the upper, the hypoconid moves between the valley between the paracone and the metacone, and the crests of the centrocrista shear past the crests extending anterolingually (cristid obliqua) and posterolingually (postcristid) from the hypoconid (**Figure 7**). One may consider how the relative heights of the paracone and metacone are related to a) the lengths of the cristid obliqua and the postcristid, and how these in turn are related to b) position of the cristid obliqua at the posterior wall of the trigonid, and c) the positions of the hypoconid and hypoconulid, two cusps connected by the postcristid. Since the postparacrista of the paracone shears against the cristid obliqua, a reduction in the height of the paracone (and thus the length of the postparacrista) may be correlated with a shorter cristid obliqua, which may in turn be associated with a labial shift of the cristid obliqua (Crompton and Hiiemae, 1970: 21; Archer, 1976; Crompton and Kielan-Jaworowska, 1978: 279). In turn, the premetacrista of the metacone shears against the postcristid of the lower molars. A larger or higher metacone results in a longer premetacrista, which may be associated with a longer postcristid. An increase in the length of the postcristid could be correlated with a lingual shift of the hypoconulid, so that it is more closely approximated to the entoconid, such that the hypoconulid is posterior to the entoconid rather than being more labially positioned (Slaughter, 1968a, 1971; Clemens, 1966, 1979: 202, instead believed that the relative positions of the hypoconulid and entoconid are due to an increase in the width of the talonid). These relationships are complex, and perhaps not all of the elements involved have been recognized. This is problematic because if only some redundant characters were recognized through an examination of functional relationships and omitted, but others were not, the data used in the phylogenetic analysis would probably be even more biased than if no redundant characters had been removed. As well, attempts to not code redundant characters may eventually reach the level of the entire molar, as the level of relationship between various features increases (Fischer, 1981). Therefore, both upper and lower molar characters are retained in this analysis, though upper molar characters make up the bulk of the data set.

Several runs of the PAUP 3.0 program were attempted, including ones in which one character was ordered, as described above, ones in which all characters were left unordered, and ones in which the successive approximations method was used. In addition, one run tested how many extra steps on the cladogram would be required if *Alphadon* s.l. was entered into the analysis as a monophyletic group. To do this, the more derived marsupial ingroup taxa were removed and *Alphadon* s.l. and the various outgroup taxa were considered alone. The resulting cladograms were then added to a run in which the more derived marsupial taxa were returned. These more derived taxa were added to the cladogram, but their positions could not change the structure of *Alphadon* s.l., in other words *Alphadon* s.l. was a monophyletic group. This run and all others performed are discussed in more detail in Chapter 4.

OUTGROUP ANALYSIS. Once characters and their various states have been designated and scored for all taxa, the polarity (plesiomorphy versus apomorphy) of these states must be established, because cladistic methodology involves the search for monophyletic groups characterized by the possession of synapomorphies, or shared derived character states. Therefore, synapomorphies must be distinguised from symplesiomorphic ("primitive" or ancestral) states. There have been several methods described for polarizing character states (see Crisci and Stuessy, 1980 and Stevens, 1980 for reviews of these methods), but the outgroup method is the one applied in this analysis. PAUP 3.0 allows for the researcher to designate outgroup taxa prior to the analysis, then reconstructs phylogenies, taking into consideration states in both the ingroup and outgroup. This is the method of global parsimony advocated by Maddison et al. (1984). The resulting most parsimonious trees can then be rooted to give the polarity of the character states.

The choice of outgroups to be used in this analysis is dependent upon the higher-level relationships of Marsupialia to other taxa. Taxa outside of the Marsupialia must be examined, because, although *Alphadon* s.l. is **not** the ancestral marsupial taxon, it is also not phylogenetically far removed from the base of the marsupial radiation. Evidence for this comes from the morphology of the some of the more plesiomorphic species assigned to *Alphadon* s.l. (*A. creber* and "*A.*" *lulli*), which closely approximate that of the hypothetical ancestral marsupial morphotype, and from the relative age of the earliest referred species (*A. creber*, upper member of the Milk River Formation, Alberta, previously the oldest North American marsupial taxon; Cifelli and Eaton (1987) have recently described a new species, *Pariadens kirtlandi* (Family Stagodontidae) from the Cenomanian of Utah). The relationship between a plesiomorphic morphology and relative age may not be absolute, but both lines of evidence should be considered.

One major problem involved in using taxa phylogenetically outside of the Marsupialia as outgroups involves the determination of the homologies of individual teeth between *Alphadon* s.l. and these outgroup taxa, including the basal eutherians, the Order

Deltatheroida Kielan-Jaworowska, 1982 and *Pappotherium*. This problem with the dental homologies arises because marsupials have an unreduced dental formula traditionally designated as **I5/4; C1/1; P3/3; M4/4**, while the general unreduced eutherian formula is **I3/3; C1/1; P4/4; M3/3** (see below for a discussion of *Prokennalestes* and other taxa, in which five premolars are present). That of the deltatheroidans is either **I?4/?1; C1/1; P3/3; M3/4** (*Deltatheridium*, Family Deltatheridiidae, Butler and Kielan-Jaworowska, 1973; Kielan-Jaworowska, 1975b; Clemens and Lillegraven, 1986) or **I?/?; C1/1; P3/3; M4/4** (*Deltatheroides*, Family Deltatheroididae, Kielan-Jaworowska, 1975b; Clemens and Lillegraven, 1986; Kielan-Jaworowska and Nessov, 1990), while the dental formula of *Pappotherium* is not confidently known, but is believed to be similar to the eutherian formula in the possession of three molars (Slaughter, 1968a, 1971; Fox, 1975) and four premolars (Slaughter, 1971). Some researchers using outgroups phylogenetically outside the Marsupialia have not discussed molar homology (Reig et al., 1987; Marshall et al., 1990, Cifelli, 1990a). Many of the characters used in the upcoming phylogenetic analysis are general, and not specific to a particular molar. In this case, dental homologies between the outgroup and ingroup taxa are not as important. Nevertheless, there are morphological trends along the molar row, for example, in the anterior width of the stylar shelf, which increases from M1 to M3 (**Figure 8**). If one is comparing the greater width of the anterior stylar shelf on the penultimate molar of a species of *Alphadon* s.l. (an M3) with the state of the anterior stylar shelf in the outgroup taxa, then the upper molars compared in these outgroups should be homologous to the marsupial M3. Hypotheses of dental homologies are often difficult to understand, and the hypothesis that accounts for the number of premolars (five) observed in several early mamalian taxa, (McKenna, 1975), uses a numbering system of the dentition different from the traditional system given above. Other authors have developed a much simpler system of homologies (Van Valen, 1974). These hypotheses of dental homology are discussed briefly below.

DENTAL HOMOLOGIES. The unreduced number of premolars for the Eutheria is traditionally given as four, but several researchers have noted that certain early eutherian taxa possess five premolars (some individuals of *Gypsonictops* (Lillegraven, 1969: Clemens, 1973: Novacek, 1977a, 1986a, b); juvenile *Kennalestes* (McKenna, 1975); possibly *Kielantherium* (Dashveg and Kielan-Jaworowska, 1984); *Otlestes* (Nessov, 1985, in Clemens and Lillegraven, 1986); *Prokennalestes* (Kielan-Jaworowska and Dashveg, 1990); and Eocene sirenians (Domning et al., 1982)). The first two examples (*Gypsonictops* and the juvenile *Kennalestes*), and the recognition of five premolars in *Peramus*, the non-tribosphenic sister taxon to the tribosphenic therians (classified in the

Infraclass Tribosphenida McKenna, 1975, which included the cohorts Marsupialia and Eutheria), led McKenna (1975) to suggest that the primitive or unreduced dental formula for the Tribosphenida **as a whole** included five premolars and three molars. From this number, eutherian and marsupial taxa lost premolars (McKenna, 1975: fig. 2) to reach the unreduced number in both (four in the eutherians and three in marsupials). Within this scheme, McKenna (1975: 28, 30) interpreted the **most posterior** premolar in the Marsupialia as P4/4, rather than the more traditional designation of P3/3, such that the P4 in *Peramus* was homologous with this P4 in the marsupials, as well as the P4 in "certain Mesozoic and later mammals such as *Kennalestes* and *Zalambdalestes*" and related taxa classified in McKenna's Magnorder Ernotheria. Further, McKenna (1975: 30) suggested that this tooth in *Peramus* is homologous with P4 in various other eutherians classified in the Cohort Epitheria. Also, the tooth traditionally designated M1/1 in marsupials was interpreted by McKenna (ibid.) as a retained or unreplaced dP5/5, such that the M2/2, M3/3, M4/4 of the Marsupialia were actually M1/1, M2/2 and M3/3, homologous with the three molars in Ernotheria, but not necessarily with other taxa in the Epitheria (the Magnorder Prepotheria, sister group to the Magnorder Ernotheria within the Epitheria).

Peramus	dP1/1	P2/2	P3/3	P4/4	P5/5	M1/1	M2/2	M3/3
Marsupialia			?	P4/4	dP5/5	M1/1	M2/2	M3/3
traditional formula				**P3/3**	**M1/1**	**M2/2**	**M3/3**	**M4/4**
Kennalestes, Zalambdalestes and their allies (Ernotheria)				P4/4	P5/5	M1/1	M2/2	M3/3

This is because McKenna (1975) suggested that within the Magnorder Prepotheria, the number of premolars present is due to a **loss** of P5/5, a retention of dP5/5 as a fully molariform tooth (M1/1), and loss of M3/3 (also Fox, 1977; Bown and Kraus, 1979, but see Novacek, 1986b, for a contrary opinion). This makes assessment of homologies with the marsupials more confusing, but for the purposes of this analysis, outgroup taxa would all be classified in the Magnorder Ernotheria (i.e., *Kennalestes*, Fox, 1977). This hypothesis implies that homologous molars in the Marsupialia and the basal Eutheria (Magnorder Ernotheria) used in this analysis (using traditional marsupial molar designation written in boldface, eutherian molars in plain text) are: **M2/2**-M1/1; **M3/3**-M2/2; **M4/M4**-M3/3.

McKenna's work does seem reasonable when considering similarities in the morphology of ultimate molars in marsupials and eutherians (**Figure 9**), and it accounts for the primitive number of premolars observed in several mammalian taxa. Many researchers have accepted five premolars as the primitive number for the Eutheria (Szalay, 1977; Schwartz, 1978; Novacek, 1977a, 1980), but others have not (Butler, 1980; Luckett and Maier, 1982). Van Valen (1974) suggested that the seven cheek teeth of placentals and marsupials (including *Deltatheridium*) were homologous to one another, such that the dP4/4 or P4/4 was homologous to the M1/1 of marsupials. Thus M2/2, M3 /3 and M4/4 in marsupials would be homologous with M1/1, M2/2 and M3/3 of placentals. Van Valen's hypothesis is similar to that of McKenna's but seems to concern itself with dental homologies after the loss of the fifth premolar (though this is not specifically stated by Van Valen), and does not interpret the marsupial M1/1 as a retained dP5/5. McKenna's hypothesis is more nearly correct in that it accounts for all five original premolars, but Van Valen's work has the benefit of simplicity, and the retention of traditional tooth designations in the Marsupialia (M1/1 rather than dP5/5), and therefore, Van Valen's homologies will be retained in this analysis. It should be noted here that Archer (1978) reevaluated the unreduced marsupial dental formula and, using morphological and ontogenetic evidence from various marsupial taxa, suggested that the marsupial deciduous cheektooth, rather than being dP3/3 (replaced by P3/3, the traditional view), was M1/1, and thus the marsupial dental formula should be reinterpreted as including P1/1-3/1, M1/1 and M2/2-5/5, such that the traditional designation of the molars (M1/1, M2/2, M3/3, M4/4) was reinterpreted as M2/2, M3/3, M4/4, M5/5. There seems to be some confusion as to the fate of M1/1; Archer (1978: 157, 160) suggests that there are two separate series of teeth (or "Zahnreihe"), including P1/1-3/3 and M1/1-M5/5, and P3/3 does not replace M1/1, so that there is no true postcanine tooth replacement in the Marsupialia. Instead, M1/1 is vestigial and resorbed before is erupts (Archer, 1982b: 446). On the other hand, Clemens and Lillegraven (1986: 74) and Marshall et al. (1990: 434) state that M1/1 is displaced by P3/3. Other authors note that M1/1 is homologous with or is the deciduous marsupial tooth (Clemens, 1979: 203; Marshall, 1987: 97; Marshall and de Muizon, 1988; Reig et al., 1987: 3), implying that M1/1 is replaced. The work of Archer has been accepted and used by some researchers (Aplin and Archer, 1987; Reig et al., 1987; Marshall, 1987; Marshall and de Muizon, 1988; Marshall et al., 1990), but not by others. The use of Archer's system in evaluating dental homologies between marsupials and eutherians would probably only serve to complicate matters, and therefore the hypothesis of Van Valen (1974) regarding these homologies will be followed here.

Molar homologies between the Marsupialia and the Deltatheroida will be discussed further below in a general discussion of the outgroup taxa used in this analysis. Hypotheses regarding the dental homologies between the Marsupialia and the Deltatheroida were based primarily on reconstructions of the dental formula of taxa such as *Deltatheridium* and *Deltatheroides*. The traditional dental formula for these taxa was given above, with the Order Deltatheroida being characterized by a dental formula including three premolars and four molars (with the loss of an upper molar in *Deltatheridium* being a derived state), and are considered homologous to the postcanine teeth in the Marsupialia. The homologies between the marsupial dentition and that of *Pappotherium* are more difficult to determine, as a complete postcanine dentition of *Pappotherium* is unknown. The most nearly complete specimen referred to this genus is SMP-SMU 61725 (**Figure 10**), which includes ultimate and penultimate molars. Whether these molars represent M3 and M4 (as in marsupials) or M2 and M3 (placentals) is difficult to determine. Since Slaughter (1968a, 1971) suggested that *Pappotherium* should be classified in the Eutheria on the basis of molar morphology, a designation of M2 and M3 would be appropriate. Fox (1975) provides additional evidence from a comparison of the crown outlines of ultimate and penultimate molars in *Deltatheroides*, *Holoclemensia* and *Potamotelses* Fox, 1972 to suggest that for *Pappotherium*, these molars are M2 and M3. Therefore, the molar homologies between *Pappotherium* and the Marsupialia will be as discussed above for the marsupials and placentals.

As indicated, a determination of dental homologies between the outgroup and ingroup taxa for this analysis is somewhat confusing. As noted above, many of the characters in this analysis will be general, or applicable to any molar in the tooth row. The remainder of this part of Chapter 2 will involve discussions of each of the outgroups included in this analysis, including the reasons why these taxa were chosen. Each outgroup used corresponds to previous hypotheses of the higher level relationships between these taxa and the Marsupialia, and in this way also acts as a test of these hypotheses.

OUTGROUP TAXA INCLUDED. For many years, *Alphadon* s.l. was considered to represent or to actually be the most primitive or plesiomorphic marsupial taxon (Clemens, 1966, 1968, 1977, 1979; McKenna, 1969; Lillegraven, 1974; Archer, 1976; Marshall, 1976; Kirsch, 1977; Fox, 1979; Szalay, 1982a, b; Woodburne, 1984; Marshall, 1987; Aplin and Archer, 1987). Work by Fox (1983, 1987a, b; Fox and Naylor, 1986; also Clemens, 1979) has suggested that the hypothetical ancestral marsupial upper molar lacked a stylar cusp C, removing *Alphadon* s.l. (whose referred species generally possess a stylar cusp C) from this position. Nevertheless, *Alphadon* s.l. is not far removed from this ancestry, especially the more plesiomorphic species assigned to *Alphadon* s.l. (Marshall et. al, 1990). Therefore, to resolve the polarity of character states within *Alphadon* s.l. it is important to look outside the Marsupialia rather than to other marsupial taxa, which will be derived in many of dental characters states relative to *Alphadon* s.l. Generally, several outgroups should be used in the determination of the character state polarities for the ingroup taxa (Maddison et al., 1984). Only four outgroup taxa will be used in this study, including two representatives of the basal Eutheria, *Prokennalestes* Kielan-Jaworowska and Dashveg, 1989 (?Aptian or Albian, Khoboor Beds, Gobi Desert, Mongolia), and *Kennalestes* Kielan-Jaworowska, 1968 (?Late Campanian, Djadokhta Formation, Gobi Desert, Mongolia). Basal eutherian taxa are used in this analysis because, in assessing the polarity of character states of the ingroup (*Alphadon* s.l., Marsupialia), one is interested in character states at the node at which the taxon Eutheria joins the cladogram, and the more plesiomorphic or basal eutherian taxa would presumably show the closest approximation to the hypothetical ancestor at this node. The two other outgroups used are members of the Order Deltatheroida Kielan-Jaworowska, 1982 (?Middle or Late Campanian, Djadokhta Formation, ?Middle or Late Campanian/Maastrichtian Barun Goyot Formation, Gobi Desert, Campanian/Maastrichtian, Oldman, Scollard and Lance formations, North America), and the North American "therian of metatherian-eutherian grade" taxon, *Pappotherium* (Albian, Paluxy Formation, Texas).

The outgroup taxa used here account for the range of recent hypotheses regarding the higher-level relationships of the metatherians and eutherians to one another and to other more distantly related taxa, and relationships of *Alphadon* s.l. to other plesiomorphic marsupial taxa (**Figure 11**). In the first of these hypotheses (Marshall et al., 1990, **Figure 11A**), Metatheria and Eutheria are sister-group taxa, with the tribotheres in an ancestral, or more appropriately, an outgroup position. Marshall et al. (1990: fig. 1) are vague about the taxa included in the tribotheres; the tribotheres were said by these researchers to be similar in composition to the tribotheres of Clemens and Lillegraven (1986) and, approximately, the Tribosphenida of McKenna (1975) and Prothero (1981), in that they include taxa whose upper molars possess a protocone occluding in a basined talonid of the lowers. However, the Tribosphenida, as used by both McKenna (1975) and Prothero (1981), includes **all** taxa possessing tribosphenic molars, including the metatherians and eutherians, and taxa such as the "therians of metatherian-eutherian grade". Marshall et al. (1990) separate the tribotheres from the metatherians and eutherians. Therefore, the tribotheres, as used by these researchers, may be more similar to the concept of Clemens and Lillegraven (1986), in which these are separated from the metatherians and eutherians, except that Clemens and Lillegraven (1986) include only certain Late Cretaceous taxa in the tribotheres (Late Cretaceous taxa were the focus of their paper). In any event, this concept does not include the deltatheroidans (Clemens and Lillegraven, 1986), and therefore (with respect to this analysis), one may presume that Marshall et al. (1990) are suggesting that the tribotheres share a closer relationship to the metatherians and eutherians than do the deltatheroidans. This is similar to the hypothesis of relationship proposed more explicitly by Cifelli (1990c, **Figure 11B**). Here, Cifelli uses character states and polarities discussed by Crompton (1971) and Fox (1975), with a resulting cladogram in which the **tribotheres** (in Cifelli's analysis, *Slaughteria* Butler, 1978, *Holoclemensia* Slaughter, 1968a, and *Pappotherium*) are more closely related to the Marsupialia and the Eutheria than are the deltatheroidans. These tribotheres are derived relative to the deltatheroidans in the loss of the distal metacristid on the lower molars (see Fox, 1975 for a description of this crest), and the possession of a complete anterior cingulum on the upper molars. This complete anterior cingulum creates two shearing surfaces on the anterior side of the upper molar (double-rank shear, Crompton, 1971). The third hypothesis (**Figure 11C**) was presented by Kielan-Jaworowska and Nessov (1990), who state that the Deltatheroida and Marsupialia are sister taxa, based on synapomorphies in the dental formula and basicranial morphology. This hypothesis is the culmination of an earlier suggestion made by Butler and Kielan-Jaworowska (1973). The final recently proposed outgroup hypothesis is that of Cifelli (1990a). In this hypothesis, Cifelli suggests that the species *Iqualadelphis lactea* Fox, 1987 (Milk River Formation, Early Campanian) is the sister group to his revised concept of *Alphadon* s.l. This suggestion is based on new specimens referred to *I. lactea* from the Kaiparowits Formation, Utah (upper Campanian) and a revised diagnosis given for this species. After examining specimens originally referred to *I. lactea*, and comparing these to specimens from the Kaiparowits Formation, this latter hypothesis is rejected (see Chapter 3 for a further discussion).

All of the outgroups involved in these hypotheses will be discussed further below. As well, taxa that are considered to be more derived than *Alphadon* s.l. (*Peradectes*, *Peratherium* and two others) will be included. Taxa that are considered derived members of the ingroup should also be used (M. V. H. Wilson, pers. comm., 1991), since a character state may be derived within *Alphadon* s.l. relative to the outgroup taxa, but may be found in other closely related marsupial groups, and would therefore be a synapomorphy for a more inclusive taxon including *Alphadon* s.l. and these other marsupials. The presence of stylar cusp C is a good example, being absent in the outgroup taxa included here, but being variously found in *Alphadon* s.l., *Peradectes* and *Peratherium*. The presence of stylar cusp C would not be a synapomorphy for *Alphadon* s.l. because of its presence in these more derived taxa. Besides *Peradectes* (recently classified along with *Alphadon* s.l. in the Cohort Alphadelphia Marshall et al., 1990) and *Peratherium* (Cohort Ameridelphia), the two other more derived marsupial taxa included are classified in the Cohort Australidelphia. Taxa from the Cohort Australidelphia are used as representatives of more derived ingroup taxa in this analysis because of the most recent reconstruction of the phylogenetic relationships of the Marsupialia described by Marshall et al. (1990: fig. 2, reproduced in **Figure 5g**). The relationships of *Alphadon* s.l. (Cohort Alphadelphia) to the cohorts Australidelphia and Ameridelphia are unresolved, and are presented as a basal trichotomy, although Marshall et al. (1990: 449) suggest that the Alphadelphia represents the basal marsupial clade. However, in strictly following the cladogram of Marshall et al. (1990), more derived taxa from both the cohorts Ameridelphia and Australidelphia must be included in the analysis.

Though taxa from all three marsupial cohorts are examined, the number of derived members of the ingroup, as well as the number of outgroup taxa included will be kept to a minimum, because of the nature of the materials being studied. Species assigned to *Alphadon* s.l. have been described on the basis of the dentition, and this restricts the types and numbers of characters that can be used in a phylogenetic analysis. Butler (1941, 1961, 1978, 1982) has commented on the susceptibility of dental characters to parallelism and convergence, which suggests that character states observed within *Alphadon* s.l. will probably be observed in other taxa, taxa most closely related to *Alphadon* s.l. (homology) as well as taxa that are not as closely related to *Alphadon* s.l. (homoplasy). The outgroups and more derived taxa used in this phylogenetic analysis must be chosen carefully so that homologous states (states observed in taxa and hypothesized to be in or derived from a state in the common ancestor of these taxa) rather than homoplastic states (not present in the common ancestor of taxa) are compared.

***KENNALESTES* AND *PROKENNALESTES*.** Until the recent work of Kielan-Jaworwoska and Nessov (1990), metatherians and eutherians were generally considered to be sister group taxa, or to share a more recent common ancestry exclusive of other groups (see Marshall, 1979; Rowe, 1986, 1988; Wible, 1991 for recent reviews). Metatherians and eutherians differ in many respects, including dental formula, basicranial morphology (i.e., Novacek, 1977b; Wible, 1990), and particularly in the female reproductive system (i.e., Lillegraven, 1969; Lillegraven et al., 1987), but also share several derived characters. This hypothesis of relationship suggests that certain basal eutherians would be appropriate outgroups to the Marsupialia and *Alphadon* s.l. *Kennalestes* and *Prokennalestes* are included as these basal representatives. Crompton and Kielan-Jaworowska (1978: fig. 1) reconstructed a hypothetical primitive eutherian upper and lower molar, and noted (ibid.: 269) that except for small differences, molars referred to *Kennalestes* closely approximate this hypothetical morphology, as do those referrred to *Prokennalestes* (Kielan-Jaworowska, 1984: 178). *Kennalestes* has been considered by several other researchers to represent one of the more primitive eutherian taxa (McKenna, 1969; Butler, 1972b, 1977, 1980; Kielan-Jaworowska, 1977, 1981; Crompton and Kielan-Jaworowska, 1978; Kielan-Jaworowska et al., 1979; Cifelli, 1983; Novacek, 1986b; Prothero et al., 1988; Carroll, 1988), but appears derived in the possession of pre- and postprotocingula along the sides of the protocone, and in the reduction of the number of incisors (four upper and three lower, Kielan-Jaworowska, 1981). *Asioryctes* Kielan-Jaworowska, 1975a, (Barun Goyot and Khermeen Tsav formations, Mongolia) possesses five upper incisors and four lower, similar to the unreduced number in the Marsupialia, and considered to be the number present in the most recent common ancestor of the marsupials and placentals (Marshall, 1979; Clemens and Lillegraven, 1986; Wible, 1991). *Asioryctes* is derived in the loss of the metaconule (Fox, 1975), and in the reduction of the stylar shelf. Both *Kennalestes* and *Asioryctes* are early eutherian taxa possessing both plesiomorphic and apomorphic character states, but since the number of outgroup taxa will be kept to a minimum in this analysis, only *Kennalestes* will be included because it generally has been better described and figured in the literature than *Asioryctes*. Upper molars referred to *Kennalestes* show similarities to the ancestral marsupial morphotype (Cifelli, 1990a; Marshall et al., 1990), including a greater transverse width to anteroposterior length ratio, such that the paracone and metacone are closely appressed on the molar occlusal surface, and a sharp and uninflated paracone and metacone, wider stylar shelf, and a low and anteroposteriorly compressed protocone (**Figure 9B**).

Prokennalestes, as well as a second taxon, *Prozalambdalestes*, as originally named by Trofimov (1974, in Beliajeva et al., 1974, as noted in Kielan-Jarowska and Dashveg, 1989), but neither figured nor described. These taxa were then *noma nuda*, but still discussed in terms of possible ancestry to *Kennalestes* and *Zalambdalestes*, respectively (McKenna, 1975; Kielan-Jaworowska, 1981, 1984; Crompton and Kielan-Jaworowska, 1978; Kielan-Jaworowska et al., 1987). Kielan-Jaworowska and Dashveg (1989) described and figured relevant materials of *Prokennalestes*, so that this taxonomic name was no longer invalid, and suggested that *Prozalambdalestes* was a junior synonym of *Prokennalestes*. *Prokennalestes* was said to be the most primitive eutherian mammal, primarily on the basis of the number of premolars (five) thought to be present in this taxon, determined from the number of premolar loci on referred mandibles (McKenna, 1975; Crompton and Kielan-Jaworowska, 1978; Kielan-Jaworowska, 1984; Kielan-Jaworowska and Dashveg, 1989). Recall that McKenna (1975) suggested that five premolars was the primitive state for the Eutheria plus Metatheria, based on the number of premolars in the Late Jurassic taxon, *Peramus*, and presumed premolar-molar homologies between *Peramus* and the eutherians and metatherians. *Prokennalestes* is morphologically similar to *Kennalestes* (Kielan-Jaworowska, 1984), so that these two taxa are appropriate outgroups, being basal taxa for the Eutheria.

ORDER DELTATHEROIDA. A more closely related ougroup taxon to the Marsupialia (and thus to *Alphadon* s.l.) was suggested by Kielan-Jaworowska and Nessov (1990) to be the Order Deltatheroida, to which are assigned the Family Deltatheridiidae (including *Deltatheridium* Gregory and Simpson, 1926) and the new Family Deltatheroididae (including *Deltatheroides* Gregory and Simpson, 1926, and cf. *Deltatheroides* sp. Fox, 1974). Also included in the Order Deltatheroida is the Genus *Sulestes* Nessov, 1985 (in Kielan-Jaworowska and Nessov, 1990), from the middle part of the Taikarshin Beds in Dzhara-Kuduk, Uzbekistan, of ?Coniacian age. This is older than other taxa referred to the Order Deltatheroida, if age assignments of the Barun Goyot and Djadhokta formations are correct. Kielan-Jaworowska and Nessov (1990) described these assignments as "best guesses" (see Lillegraven and McKenna, 1986, for an excellent review of this problem).

The deltatheroidans (a term used throughout and considered to be equivalent to the Order Deltatheroida of Kielan-Jaworowska, 1982 and Kielan-Jaworowska and Nessov, 1990) were originally described on the basis of poorly preserved specimens from Mongolia (Gregory and Simpson, 1926), including partial skulls and associated lower dentitions (*Deltatheridium pretrituberculare*) and a partial skull preserving the upper dentition (*Deltatheroides cretacicus*). Later specimens collected by the Polish-Mongolian expeditions in the Gobi Desert included skulls with associated upper and lower dentitions in a better state of preservation (Kielan-Jaworowska, 1969, 1975a, b). For many years, the phylogenetic relationships of the deltatheroidans to other taxa were not well resolved, partly due to the nature and poor preservation of the materials collected, and partly due to an uncertainty regarding the dental formula of these taxa, particularly in terms of the numbers of premolars and molars present. This uncertainty has resulted in a long history of unstable deltatheroidan classification. Gregory and Simpson (1926) interpreted the dental formula of

Deltatheridium as including **four** premolars (with only three premolars present on the actual specimen, the first premolar was said to be missing) and three molars, and that of *Deltatheroides* including four premolars and three molars, all of which were present. Similarities in the numbers of premolars and molars led Gregory and Simpson (ibid.) to classify these taxa as eutherians (the general dental formula of the eutherians includes P4/4 and M3/3), and more specifically as the Family Deltatheridiidae, Order Insectivora. Comparisons were made to the palaeoryctid insectivore *Didelphodus* (also assigned to the Family Deltatheridiidae by Gregory and Simpson, 1926; Simpson, 1928a) and to the Creodonta, with the Mongolian deltatheroidans considered to be ancestral to the creodonts and to dilambdodont insectivores (Gregory and Simpson, 1926: 6). Simpson (1928a: 8) suggested that the members of the Family Deltatheridiidae showed dental similarites to *Palaeoryctes* in that upper molars of both were thought to show a connate paracone and metacone (joined at the bases and for a part of their length), approaching the condition seen in zalambdodont insectivores. Simpson (1928a: 9) also suggested a relationship to the Creodonta (also Kretzoi, 1945, as discussed in Van Valen, 1969), such that the Deltatheridiidae was near the base of a "focal Asiatic proto-creodont group, within the Insectivora." However, by 1931, Simpson had classified the Creodonta within the Order Carnivora (based on suggestions by Matthew (1929), and other earlier workers (in MacIntyre, 1966)), with the Deltatheridiidae being assigned to the Superfamily Deltatheridioidea, Order Insectivora. In Simpson's (1945: 177) extensive classification of the Mammalia, the Family Deltatheridiidae remained in the Order Insectivora, with Simpson noting that this family "seem[s] to stand midway between the "zalambdodonts" and "dilambdodonts"[insectivores]".

Simpson (1931, 1945) had classified the Family Palaeoryctidae (and *Palaeoryctes*) in the Superfamily Tenrecoidea, separate from the Deltatheridiidae, because of similarities between the upper molars of *Palaeoryctes* to *Potamogale*, a Recent West African insectivore classified in the Tenrecoidea, such that *Palaeoryctes* was thought to be ancestral to *Potamogale*. McDowell (1958: 180) however, denied this ancestry and any relationship between *Palaeoryctes* and *Potamogale*, and synonymized the Family Deltatheridiidae with the Family Palaeoryctidae, retaining the Palaeoryctidae in the Order Insectivora. Thus, McDowell (ibid.) resurrected the hypothesis of a close relationship between *Palaeoryctes* and the Deltatheridiidae. McKenna (1960) assigned the Palaeoryctidae to the Superfamily Deltatheridioidea, and classified this taxon in Order Carnivora, suborder Creodonta. Soon after though, McKenna et al. (1962) returned the Deltatheridioidea to the Order Insectivora, but noted that this did not preclude a relationship to the oxyaenid creodonts.

Van Valen (1965, 1966, 1967) restated the hypothesis of a close relationship between certain deltatheroidans and the Creodonta by erecting a new order, Deltatheridia Van Valen, 1965, based on the Palaeoryctidae, as well as the Hyaenodontidae and the Oxyaenidae, two families usually classified in the Creodonta. The Deltatheridiidae were included in the Palaeoryctidae, as suggested by McDowell (1958; also McKenna, 1969; Kielan-Jaworowska, 1975b). Van Valen (1966: 101) considered the Order Deltatheridia to be separate from the Carnivora and Insectivora, contrary to earlier classifications. Van Valen's classification has been used by Lillegraven (1969), Mellett (1969) and Rich (1971), but criticized by MacIntyre (1966), Szalay (1968a, b, 1969), and McKenna (1969), who believed that the Palaeoryctidae should have remained in the Order Insectivora. By 1971, Van Valen had split the Deltatheridia into the "insectivorous Deltatheridia", classified in the Order Insectivora, and the "carnivorous Deltatheridia", classified in the Order Hyaenodonta (Van Valen, 1971: 423). The ordinal name Deltatheridia was no longer used (also Van Valen, 1974), and the Palaeoryctidae (=Family Deltatheriidae) was returned to the Order Insectivora. Szalay and McKenna (1971) and McKenna et al. (1971) retained this classification and modified previous interpretations of the dental formula of *Deltatheridium* (four premolars (three present, one missing) and three molars (Gregory and Simpson, 1926)) by suggesting all premolars and molars were present, and that the tooth previously considered to be the first molar was actually semimolariform and more similar to an ultimate premolar; therefore, *Deltatheridium* possessed four premolars and two molars.

All classifications and determinations of dental formulae discussed above were based on the poorly preserved materials originally examined by Gregory and Simpson (1926). Butler and Kielan-Jarowowska (1973) were able to study new materials collected by the Polish-Mongolian expeditions in the Gobi Desert and from these, determined that *Deltatheridium* approached a marsupial dental formula (3/3 premolars and 4/4 molars), with three upper and lower premolars (no missing premolar), and three upper and four lower molars. The fourth upper molar in *Deltatheridium* was considered by these authors to be lost. Butler and Kielan-Jarowowska (ibid.) noted that the semimolariform tooth in *Deltatheridium* described as the last premolar by McKenna et al. (1971) is similar to the next most posterior tooth, an undoubted molar, and that there is no reduction of the metacone or the talonid basin on these "semimolariform" teeth. Butler and Kielan-Jarowowska (ibid.) stated that no Cretaceous or Paleocene eutherian shows as high a degree of molarization on the last premolar (P4/4), and that this tooth is better interpreted as a molar, contrary to McKenna et al. (1971). *Deltatheroides* was said to have three upper and lower premolars, and four upper and lower molars. The dental formula of the Family Deltatheriidae, including *Deltatheridium* and *Deltatheroides*, was given by Butler and Kielan-Jarowowska (1973) as ?4/? 1/1 3/3 3-4/4, which is more similar to that of marsupials (5/4 1/1 3/3 4/4) than eutherians (3/3 1/1 4/4 3/3), so that *Deltatheridium* and *Deltatheroides* should be removed from the Family Palaeoryctidae (the affinities of *Deltatheridium* to the Palaeoryctidae had already been questioned by Butler (1972)). Considering that previous hypotheses of the relationships of *Deltatheridium* and *Deltatheroides* included the Insectivora and/or the Creodonta, the demonstration by Butler and Kielan-Jarowowska (ibid.) that these Mongolian taxa showed similarities to the Marsupialia was a radical one, indeed. However, because of the loss of the fourth upper molar in *Deltatheridium* and other similarities in skull morphology to *Kennalestes*, Butler and Kielan-Jarowowska (1973) classified the Family Deltatheriidae in the "theria of metatherian-eutherian grade" (also Fox, 1974, 1975; Kielan-Jarowowska, 1975; Butler, 1977; Crompton and Kielan-Jarowowska, 1978).

Several authors have tried to resolve the phylogenetic relationships of taxa classified in the "theria of metatherian-eutherian grade" (including the Family Deltatheriidae) to one another and to other taxa, particularly the metatherians and eutherians. Turnbull (1971) named a new taxon, Cohort Tribosphenata, equal in rank to his cohorts Marsupiata and Placentata. The Tribosphenata included the Order Tribosphena (including *Pappotherium* and *Holoclemensia*), and the Order Zalambdodonta, to which were assigned *Deltatheridium*, *Palaeoryctes*, as well as zalambdomorphic marsupials and placentals. *Deltatheridium* and *Palaeoryctes* were thought to represent the early stages of development leading to the zalambdodont morphology (Vandebroek, 1961). Butler (1978, also Kielan-Jaworowska, 1982) criticized Turnbull's use of the taxon Zalambdodonta, since he (Butler, 1972b) had shown that zalambdodont molars had been derived independently several times from a dilambdodont pattern, and thus the Zalambdodonta was a polyphyletic taxon. Butler (1978) provided a new classification for the "theria of metatherian-eutherian grade", by classifying taxa from this grade in the Infraclass Tribotheria (again equal in rank to the metatherians and eutherians), including the Order Aegialodontia (families Aegialodontidae, Kermackidae, Deltatheriidae, and Aegialodontia *incertae sedis* (for *Potamotelses* Fox, 1972) and the Order Pappotherida. *Aegialodon* Kermack, Lees and Mussett, 1965 (Purbeck fauna, Early Cretaceous, England), classified in the Family Aegialodontidae, is known from a single lower molar, and is the earliest taxon possessing a tribosphenic dentition (based on the pattern of shear surfaces in the talonid of the referred lower molar). Butler (ibid.) noted that some members of the Infraclass Tribotheria had given rise to the Metatheria and the Eutheria (i.e., *Aegialodon*), but that others, like the Pappotherida and Deltatheriidae, did not. Nevertheless, Butler (ibid.) still classified the Deltatheriidae in the Order Aegialodontia, but the relationships of the Deltatheriidae to other taxa were unclear. Fox (1975) also discussed a close relationship between *Aegialodon*, *Potamotelses* and the Deltatheriidae, and suggested that these three might be included in a taxon which included the common ancestors of the Metatheria and Eutheria. This hypothesis appears in a classification (Fox, 1980), which is similar to Butler's in retaining the Infraclass Tribotheria and the Order Aegialodontia to include the Aegialodontinae, Deltatheriidae, and *Potamotelses*.

Even though Turnbull (1971), Butler (1978) and Fox (1980) provided revised classifications for the "therians of metatherian-eutherian grade", and gave this group equal taxonomic rank to the Metatheria and Eutheria, it must be stressed that the relationships of the included taxa to one another and to the Metatheria and Eutheria still were not adequately resolved. Kielan-Jaworowska (1982: 372) criticized Butler's classification and his use of the taxon Tribotheria, suggesting that this was not a natural group because "[t]he Pappotherida and the Deltatheriidae... arose in my opinion from the Family Aegialodontinae as separate lines, parallel to the Marsupialia and Eutheria.". Butler (1978) had already suggested this, as discussed above. Kielan-Jaworowska (1982) removed the Family Deltatheriidae to a new order, Deltatheroida, of equal rank to the orders Aegialodontia and Pappotherida, with all three being placed in an Infraclass *incertae sedis*. Kielan-Jaworowska (1982) did not assign these taxa to an infraclass because they were considered to be insufficiently known. However, other researchers (Clemens and Lillegraven, 1986; Kemp, 1988) have favored giving the deltatheroidans an infraclass rank equal to that of the marsupials and placentals, and Clemens and Lillegraven (1986) suggested that the deltatheroidans are distinguished from these taxa in the possession of a marsupial dental formula combined with more typical eutherian molar characters.

Hoffstetter (1973, 1975, 1980), on the other hand, had maintained that the deltatheroidans were marsupials, mostly on the basis of similarities in dental formula, and now this hypothesis has been examined again by Kielan-Jaworowska and Nessov (1990). Kielan-Jaworowska and Nessov (1990) referred new materials to *Sulestes* Nessov, 1985 (Family Deltatheriidae), and classified the Deltatheriidae, and a new family, Deltatheroididae (*Deltatheroides*, cf. *Deltatheroides*) in the Order Deltatheroida (Kielan-Jaworowska, 1982). Kielan-Jaworowska and Nessov (1990: 7) suggest that the deltatheroidans are the most closely related or sister group to the Marsupialia, based on several shared derived characters, such as the dental formula, and the "uniquely metatherian structure of the basicranial region", including an auditory bulla composed of the alisphenoid, the participation of the jugal in the glenoid fossa, and in the position of the postglenoid foramen. As well, a distinct morphological break between the premolars and molars is mentioned in the differential diagnosis presented for the Order Deltatheroida. All of these characters will be discussed in turn below, with characters of the skull for the basal eutherians *Kennalestes* and *Asioryctes* (skull material of *Prokennalestes* has not been described) also being described at this time. *Asioryctes* is not included in the upcoming phylogenetic analysis, but Kielan-Jaworowska has described skull material from *Asioryctes* and*Kennalestes*, so that using information from both will only add to the evidence presented in the comparisons below.

The generalized dental formula of eutherians relative to metatherians has already been described, and it appears that the possession of three premolars and four molars is a synapomorphy for the deltatheroidans and marsupials, as suggested by Kielan-Jaworowska and Nessov (1990). Another potential synapomorphy involves the morphology of the premolars and molars. In eutherians, the more posterior premolars are submolariform, being morphologically similar to the molars. In marsupials and the deltatheroidans, there is a sharp morphological break between these two, so that the premolars show very little similarity to the molars. However, Clemens and Lillegraven (1986) favor an interpretation in which the eutherian condition is derived and the marsupial-deltatheroidan condition as plesiomorphic, because, as they state, this hypothesis would require the parallel evolution of submolariform premolars in only three distinct groups of therians, including *Shuotherium* Chow and Rich, 1982, *Peramus* (both non-tribosphenic taxa) and the eutherians (which share a common ancestry with the marsupials and perhaps the deltatheroidans). If the eutherian condition is considered plesiomorphic, then the parallel evolution of the sharp morphological break between the premolars and molars would need to be hypothesized for the deltatheroidans and marsupials and for several non-tribosphenic taxa, including *Amphitherium*, dryolestids, and paurodonts (Clemens and Lillegraven, 1986).

An examination of figures of upper and lower jaws of *Peramus* (Clemens and Mills, 1971; Kraus, 1979: fig. 8.2), and following the suggestion that there are five premolars in *Peramus* (McKenna, 1975), suggest instead that there is a sharp morphological break between the premolars and molars in this genus (contrary also to Van

Valen, 1974), as well as in other taxa assigned to the Eupantotheria (Kraus, 1979; Clemens and Lillegraven, 1986). As well, where premolars are known for members of the "theria of metatherian-eutherian grade" (Patterson, 1956: fig. 2; Slaughter, 1971: plate 9), they are nonmolariform. Since all these taxa would be even more distantly related outgroups to the Marsupialia (see classifications of McKenna, 1975; Prothero, 1981 for relationships of the non-tribosphenic therians), the sharp morphological break between the premolars and molars would be a symplesiomorphy for the deltatheroidans and the marsupials, while semimolariform premolars would be a synapomorphy for the Eutheria, convergently acquired in *Shuotherium*, as suggested by Clemens and Lillegraven (1986).

With regards to the alisphenoid auditory bulla, Kielan-Jaworowska and Nessov (1990) note that the alisphenoid participates in the bulla in some insectivores and the Macroscelida (Novacek, 1977b; Marshall, 1979), but that in these the alisphenoid contributes to only a small portion of the bulla, the remainder being composed of bones like the [ento]tympanic and the ectotympanic. The alisphenoid is absent from the bulla in the majority of eutherians, including the Early Cretaceous taxa from Mongolia (Kielan-Jaworowska, 1981, 1984) used as outgroups in this analysis. For the Deltatheroida, Kielan-Jaworowska and Nessov (1990) make reference to a photo of a well preserved skull from beds correlatable to the Nemgt Formation (?upper Campanian/?lower Maastrichtian) in Gurlin Cav, Gobi Desert. On this skull is preserved a ventral process of the posterior part of the alisphenoid, broken, but still 3 mm long, which Kielan-Jaworowska and Nessov (1990: 7) interpret as contributing to the bulla, such that deltatheroidans show "at least an incipient alisphenoid bulla". The participation of the alisphenoid in the bulla would then be a synapomorphy for the deltatheroidans plus the Marsupialia. As well, the Gurlin Cav skull is said by Kielan-Jaworowska and Nessov (ibid.) to show other similarities to the basicranial region of marsupials (specifically *Didelphis*), including a contribution of the jugal to the glenoid fossa, and the position of the postglenoid foramen. The contribution of the jugal to the glenoid fossa is suggested to be a synapomorphy for the marsupials by Marshall et al. (1990), but has also been observed in Early Cretaceous Mongolian eutherians such as *Kennalestes* and *Asioryctes* (Kielan-Jaworowska, 1975a: 7, 1981: 56, 61, but see Kielan-Jaworowska, 1984: fig. 1), and other eutherians, such as hyraxes and some rodents (Marshall, 1979). Kielan-Jaworowska (1975b: 122) had already noted a contribution of the jugal to the glenoid in *Deltatheridium*. Marshall et al. (1990: fig. 1) suggest that the state for the Marsupialia involves a jugal which participates as a prominent ventral crest along the anterolateral border of the glenoid fossa (also Clemens, 1979). Kielan-Jaworowska (1981, 1984) does not describe (nor adequately figure) the manner in which the jugal participates in the glenoid fossa in *Kennalestes* and *Asioryctes*, only noting that it extends back to this fossa (in a personal communication to Clemens (in Clemens, 1979), Kielan-Jaworowska states that the jugal does not form a preglenoid crest in *Asioryctes*). Kielan-Jaworowska and Nessov (1990) do not discuss whether the jugal forms a ventral ridge on the Gurlin Cav skull or in *Deltatheridium* (Kielan-Jaworowska, 1975b). Thus, the participation of the jugal in the glenoid fossa may be homologous for the eutherians, deltatheroidans and marsupials (Marshall, 1979), and is therefore a symplesiomorphy for the more inclusive deltatheroidan and marsupial group. If it can be shown that the jugal forms a crest along the anterolateral border of the glenoid fossa in the Gurlin Cav skull and other deltatheroidans, but not in *Asioryctes* (see note above) and *Kennalestes*, this state would possibly be a synapomorphy for the deltatheroidans plus the metatherians.

The postglenoid foramen on the Gurlin Cav skull was suggested to be similar in position to that for *Didelphis* (Kielan-Jaworowska and Nessov, 1990: 7), where it is small, posterior to the glenoid fossa, and shifted medially (Wible, 1990: fig.1). In diagrams of *Kennalestes* and *Asioryctes* (Kielan-Jaworowska, 1981: figs. 3, 6), this foramen is larger (possibly due to preparation, ibid.: 39), and also appears to be posteromedially positioned relative to the glenoid fossa (though damage to the glenoid fossa in these figures makes this difficult to determine). More important than the position of the postglenoid foramen are the vessels which pass through it. Wible (1990) stated that the veins passing through the postglenoid foramen in marsupials (the sphenoparietal emissary vein) and placentals (the capsuloparietal emissary vein) are not homologous, and that these veins and the postglenoid foramina through which they pass may be convergently acquired in these two groups. Wible (1987, 1990) also notes that an additional, neomorphic artery passes through the postglenoid foramen in marsupials, and that the absence (or reduction) of a stapedial artery is a synapomorphy of the marsupials (also Archer, 1976; Archibald, 1979; Presley, 1979, Kielan-Jaworowska, 1981). Kielan-Jaworowska (1981: 57) suggests that *Kennalestes*, and less certainly, *Asioryctes*, possessed a stapedial artery (also Wible, 1987, 1990), but does not comment on which veins (sphenoparietal emissary vein or capsuloparietal emissary vein) may pass through the postglenoid foramen in these taxa. As well, Kielan-Jaworowska and Nessov (1990) do not comment on what veins pass through the postglenoid foramen in the Gurlin Cav skull, or whether a stapedial artery was present or absent. Further study of the Gurlin Cav skull, and materials of *Kennalestes* and *Asioryctes* may resolve these questions, and provide important additional evidence for a sister group relationship between the deltatheroidans and the marsupials, separate from the basal eutherians. Until that time, a similarity in the position of the postglenoid fossa is not considered to be a synapomorphy for the deltatheroidans plus the marsupials, since the homologies of the fossa, and the vessels that pass through this fossa in these taxa are uncertain.

After a consideration of the similarites said to be shared by marsupials and the deltatheroidans (Kielan-Jaworowska and Nessov, 1990), the two that appear to be synapomorphies are the dental formula, including three premolars and four molars, and the incipient presence of an alisphenoid bulla. As more evidence is obtained from basicranium of deltatheroidans, additional synapomorphies shared by these two taxa may be found. A close relationship of the deltatheroidans to other members of the Aegialodontia, as suggested by Butler (1978) and Fox (1980), is not followed here, nor was it accepted by Kielan-Jaworowska and Nessov (1990), who remove the deltatheroidans from the Aegialodontia. These authors note that the Aegialodontidae (*Aegialodon*) differ from the deltatheroidans in several features, including the dental formula. The only similarity shared between the two is a metaconid that is reduced and smaller than the paraconid. This state is also seen in the Stagodontidae, and is not a synapomorphy for the deltatheroidans and the Aegialodontidae. As well, *Potamotelses* is not related to the deltatheroidans contrary to Fox (1972), and is not classfied in the Order Deltatheroida. Upper molars of *Potamotelses* have a narrower stylar shelf, a relatively anteroposteriorly longer and transversely shorter protocone, a paracone that is closer in height to the metacone, and a poorly developed posterior stylar shelf. The metaconid is small in both taxa, but less so in *Potamotelses*.

Kielan-Jaworowska and Nessov (1990) suggested within the Marsupialia, taxa referred to the Stagodontidae show the greatest similarity to taxa assigned to the Deltatheroida, including an emphasis on postvallum-prevallid shear, as expressed in the more strongly developed postmetacrista and paracristid on the upper and lower molars repsectively, and in the reduction of the metaconid relative to the paraconid (also Butler and Kielan-Jaworowska, 1973; Kielan-Jaworowska, 1975b; Hoffstetter, 1980). A closer examination of upper and lower molars referred to these two taxa suggests that the molar structures involved in the postvallum-prevallid shear are, in fact, dissimilar, and not indicative of any closer relationship between the Stagodontidae and the Deltatheroidea (relative to the Stagodontidae and other marsupial taxa). In the deltatheroidans, the metacone is reduced relative to the paracone but the posterior stylar shelf is still very well developed, with the postmetacrista being extended posteriorly to a degree (Kielan-Jaworowska, 1975b: fig. 1). This degree of posterior development is not seen in the

Family Stagodontidae (Simpson, 1929: fig. 45), instead, the postmetacrista is more labially oriented, with little or no posterior orientation. As well, the metacone is larger and taller than the paracone in the Stagodontidae, for example, on upper molars referred to *Didelphodon* Marsh, 1889 (Clemens, 1966: fig. 52a, b; 1968), this being opposite to the condition in deltatheroidans. Kielan-Jaworowska and Nessov (1990) suggest that the paracone is larger than the metacone in both the stagodontids and the deltatheroidans, which is incorrect. On lower molars of both taxa, the paraconid is relatively larger than the metaconid, especially so for the Stagodontidae, where the paraconid and protoconid are subequal in height (Clemens, 1966). This increase in the height of the paraconid will increase the length of the paracristid, which is correlated with a longer shearing surface on the upper molars, namely, the postmetacrista. On other taxa emphasizing postvallum-prevallid shear, the paraconid will also be shifted anteriorly, increasing the length of the paracristid, for example, in *Herpetotherium fugax* (Fox, 1983: fig. 2b), and *Hondadelphys fieldsi* Marshall, 1976 (fig. 6). On lower molars of the oldest known stagodontid, *Pariadens kirklandi* Cifelli and Eaton, 1987, the paraconid is shifted anteriorly, but in remaining stagodontids, the trigonids are anteroposteriorly compressed (Clemens, 1966; Fox and Naylor, 1986: fig. 9; Marshall et al., 1990). The paraconid appears to be shifted more anteriorly on figured lower molars of *Deltatheridium pretrituberculare tardum* Kielan-Jaworowska, 1975b (fig. 5). It is suggested (somewhat tentatively), that while the emphasis on postvallum-prevallid shear involves the relatively larger paraconid in both the deltatheroidans and the stagodontids, in the deltatheroidans, the development of increased prevallid shear also invovles an anterior shift of the paraconid. As well, in the stagodontids the development of the postvallum component involves a larger or taller metacone, while the postmetacrista is not posteriorly oriented and the posterior shelf is not as strongly developed in this direction. In the deltatheroidans, the postvallum component does involve an increased development of the posterior stylar shelf, including a more posteriorly oriented postmetacrista. The metacone is reduced relative to the paracone, and does not contribute to the emphasized postvallum component. These differences suggest that the emphasis on postvallum-prevallid shear was developed convergently in these taxa and is not indicative of a close relationship. Van Valen (1974) also suggested that the Stagodontidae and *Deltatheridium* were not as closely related, since stylar cusps observed in most marsupials (B and D) are observed on upper molars of *Didelphodon* (Family Stagodontidae), but not in *Deltatheridium*.

Certain synapomorphies suggest that the deltatheroidans share a sister group relationship with the Marsupialia, but lack other synapomorphies of the Marsupialia, including the “twinning” of the hypoconulid and entoconid on the lower molars. As well, the deltatheroidans (i.e. *Deltatheridium pretrituberculare tardum*) retain certain plesiomorphies that have been lost in taxa assigned to the "theria of metatherian-eutherian grade" (*Slaughteria*, *Holoclemensia* and *Pappotherium*), including a the presence of a distal metacristid and an incomplete anterior cingulum (Kielan-Jaworowska, 1975b; Fox, 1975; Cifelli, 1990c). The retention of these plesiomorphies led Cifelli (1990c) to reconstruct a phylogeny in which the "therians of metatherian-eutherian grade" were more closely related to the clade containing Marsupialia and Eutheria than were the deltatheroidans. Since there is evidence for the phylogenies of both Kielan-Jaworowska and Nessov (1990) and Cifelli (1990c), a representative of the "therians of metatherian-eutherian grade" should be included in this analysis as an outgroup taxon.

THE "THERIANS OF METATHERIAN-EUTHERIAN GRADE". *Holoclemensia* (**Figure 10**) was classified in the Marsupialia by Slaughter (1968a, b, 1971), based on the presence of a large stylar cusp C at the deepest portion of the ectoflexus, the greater height of the metacone relative to the paracone, and the relative positions of the hypoconulid and entoconid. On marsupial upper molars, the metacone will either be the same size and height as the paracone (*Alphadon* s.l.), or it will be larger (other more derived marsupial taxa). The metacone on upper molars referred to *Holoclemensia* is smaller than the paracone, but Slaughter (ibid.) suggested that this metacone was larger than that on upper molars of *Pappotherium*, a taxon Slaughter (1968c) referred to the Eutheria, and therefore the state in *Holoclemensia* marked the beginning of a trend towards the marsupial condition of equal or larger metacones, relative to the paracone. Slaughter (1968a, 1971) related this relatively larger metacone in *Holoclemensia*, as a trend towards the marsupial condition, to the morphology of the referred lower molar, on which the hypoconulid was said to be closer to the entoconid than to the hypoconid. Slaughter (ibid.) suggested that the length of the anterior face of metacone (the premetacrista) was related to the positions of the hypoconulid and entoconid, such that an increase in the size or height of the metacone would "crowd" the hypoconulid and entoconid, as seen in the twinning of these cusps in the Marsupialia. Therefore, the larger metacone in *Holoclemensia*, relative to the state of this cusp in *Pappotherium*, was correlated by Slaughter to the relative positions of the hypoconulid and the entoconid in *Holoclemensia*, which provided additional evidence for the assignment of *Holoclemensia* to the Marsupialia. Several researchers have supported Slaughter's classification of *Holoclemensia* (Clemens, 1971a; Sige, 1972; Lillegraven, 1974; Russell, 1975; Crompton and Kielan-Jaworowska, 1978; Fox, 1975, 1980; Slaughter, 1981; Aplin and Archer, 1987), and therefore it may appear that

Holoclemensia is an appropriate "therian of metatherian-eutherian grade" to use as an outgroup in this analysis. However, several workers have not followed Slaughter's classification (Turnbull, 1971; Tedford, 1974; Butler, 1978; Kielan-Jaworowska et al., 1979; Kielan-Jaworowska, 1982; Jacobs et al., 1989), and a reexamination of relevant materials by Cifelli (1990a) led him to state that the metacone was relatively larger on upper molars of *Pappotherium* than on *Holoclemensia* (contrary to Slaughter's findings), and that the hypoconulid and entoconid on the lower molar referred by Slaughter to *Holoclemensia* did not seem any more twinned than on any other "therian of metatherian-eutherian grade", or on lower molars of the deltatheroidans or various Late Cretaceous eutherians (also Jacobs et al., 1989). Therefore, Cifelli rejected Slaughter's classification entirely, and *Holoclemensia* will not be included as an outgroup in this analysis.

Pappotherium is a "therian of metatherian-eutherian grade" that is known from upper and lower molar material, and is included as an outgroup in this analysis, as a representative of this grade taxon. The use of the term "representative" is misleading here, since there is a wide range of morphologies referred to the "therians of metatherian-eutherian grade", and the relationships of these to one another and to other taxa are poorly resolved. Nevertheless, Cifelli's hypothesis of higher-level relationships relative to the Marsupialia must be included here, so that some taxon from this grade must be chosen as an outgroup.

Upper molars referred to *Pappotherium pattersoni* (including the holotype, SMP-SMU 61725, **Figure 10**) possess a paracone that is larger than the metacone, a wide stylar shelf both anteriorly and posteriorly, a deep ectoflexus, a cusp on the postmetacrista (Slaughter, 1971; Fox, 1975), but lack stylar cusps C and most likely, cusp D. These are states seen in basal eutherians, including those used as outgroups in this analysis, but are also seen on upper molars referred to the Order Deltatheroida. Upper molars of *P. pattersoni* are also similar to those referred to the deltatheroidans in possessing conules that are not "winged", or that lack internal cristae. The basal eutherians used as outgroups in this phylogenetic analysis all possess "winged" conules on the upper molars. One point of difference between *P. pattersoni* and the deltatheroidans is that in the former taxon, upper molars have a complete anterior cingulum and lower molars have lost the distal metacristid. *Pappotherium pattersoni* is not referred to the Eutheria in this analysis because of the lack of "winged" conules and because morphological similarities shared with eutherians are also shared with the deltatheroidans. Instead, *P. pattersoni* is retained as a member of the "therians of metatherian-eutherian grade". It is important to note that in certain figures of the holotype of *P. pattersoni*, (i.e. Slaughter, 1971: fig. 7b), the posterior shelf is drawn as being much narrower than the anterior stylar shelf. A photograph of this holotype (Slaughter, 1971: fig. 8e), other figures of these molars (**Figure 10**, also Fox, 1971: fig. 1A; Crompton and Kielan-Jaworowska, 1978: fig. 4A), and an examination of a cast of the holotype indicate that instead, the posterior shelf is nearly equal in width to the anterior.

INCLUDED INGROUP TAXA OTHER THAN *ALPHADON* S.L. The relationships of other marsupial taxa to *Alphadon* s.l. are poorly resolved (Szalay, 1982a, b; Reig et al., 1985, 1987; Marshall, 1987; Aplin and Archer, 1987). being best exemplified in the recent cladogram produced by Marshall et al. (1990: fig. 2), and in the development of the metataxon Peradectini (Crochet, 1979, 1980; =Family Peradectidae, Reig et al., 1985, 1987) to include *Alphadon* s.l., *Peradectes*, and other Late Cretaceous and Early Tertiary marsupial taxa lacking the synapomorphies of other marsupial groups. Marshall et al. (1990) classified *Peradectes* and *Alphadon* s.l. (along with these other Late Cretaceous and Early Tertiary taxa) in the Cohort Alphadelphia, equal in taxonomic rank to the cohorts Ameridelphia (north and South American taxa) and Australidelphia (Australian, North and South American taxa). The relationships of these three cohorts to one another is expressed as a trichotomy, such that no two cohorts are more closely related to one another than either are to the third, even though Marshall et al. (1990) note that Alphadelphia is the basal marsupial clade. Strictly from their given cladogram (ibid.: fig. 2), *Alphadon* s.l. is as closely related to members of the Ameridelphia as it is to members of the Australidelphia, and therefore, any phylogenetic analysis examining the relationships and character distributions of more derived taxa relative to *Alphadon* s.l. must include taxa from both of these cohorts. With regards to the Australidelphia, Archer (1976a) described two new taxa from the Etadunna Formation (Middle Miocene) of central South Australia, *Ankotarinja tirarensis* and *Keeuna woodburnei*. Archer (1976a) classified *Ankotarinja* as ?Dasyuridae because of similarities in upper and lower molar morphology to various didelphids and dasyurids and suggested that among the didelphids, *Alphadon* s.l. showed some similarity to *Ankotarinja*, and that *A. tirarensis* provided evidence for a relationship between Late Cretaceous didelphids like *Alphadon* s.l. and modern dasyurids (Archer, 1982a: 427). Archer (1976a: 67) noted that *K. woodburnei* was more similar to the dasyurids than the didelphids, and also made comparisons to *Peradectes* and *Peratherium*. An examination of figures of both *K. woodburnei* and *A. tirarensis* (Archer, 1976a: fig. 3, 4, 7, and 8) does suggest several similarities, particularly to *Peratherium*. Since Archer (1976a) suggested a relationship between *Alphadon* s.l. and *Ankotarinja tirarensis*, *A. tirarensis* is included in this phylogenetic analysis; however, the greater similarity to taxa like *Peratherium* suggests that *A. tirarensis* shares a closer relationship this taxon. *Keeuna woodburnei* is not included in the analysis because of general similarities between this species and *A. tirarensis* and because of the phylogenetic position of a third taxon, *Andinodelphys cochabambensis* Marshall and de Muizon, 1988 (El Molino Formation, ?Late Cretaceous, Bolivia), in the cladogram of Marshall et al. (1990).

In this cladogram, *Andinodelphys cochabambensis* is positioned at the most basal node of the Cohort Australidelphia. Marshall et al. (1990: 460) noted several similarites between this South American species and *Ankotarinja tirarensis*, including a metacone larger and higher than the paracone, twinned stylar cusps in the C position, and a metaconule larger than the protoconule. Because of these similarities, which are not shared by any other South American marsupial taxon, *A. cochabambensis* was assigned to the Cohort Australidelphia. This species retains what Marshall et al. (1990) consider to be plesiomorphic features, including a straight centrocrista and an anteroposteriorly compressed protocone; therefore *A. cochabambensis* is placed at the base of the australidelphine radiation. *Andinodelphys cochabambensis* is considered to be a suitable taxon for inclusion in this analysis because of its basal position, and its phylogenetic relationship to other australadelphines, especially *Ankotarinja tirarensis*.

Other more derived taxa included in this phylogenetic analysis are classified in the Cohort Alphadelphia (*Peradectes* (?Late Cretaceous, S.Am.; Early Paleocene-Middle Olig., N.Am.; Middle Paleocene- Early Eocene, Europe)) and the Cohort Ameridelphia (*Peratherium* (Early Eocene-Early Miocene, N. Am.; Early Eocene-Late Oligocene, Europe; Early Oligocene, Africa)) by Marshall et al. (1990). *Peradectes* and *Peratherium* are included in this phylogenetic analysis because various authors have suggested at one time or another, some form of close relationship between either *Alphadon* s.l. and *Peradectes*, *Peradectes* and *Peratherium* (Clemens, 1968; Krishtalka and Stucky, 1983b, Montellano, 1986) or *Alphadon* s.l. and *Peratherium* (Russell, 1975, 1984). For example, Russell (1975: 155, 1984) noted that *Alphadon* s.l. was possibly ancestral to *Peratherium*. This suggestion of ancestry was presumably based on similarities between some specimens assigned to *Alphadon marshi* (i.e. UALVP 2846, Lillegraven, 1969: fig. 15.3) and *Peratherium*. These similarities involve dilambdodont upper molars, and have also been discussed by Cifelli (1990a). The taxonomic revision of *A. marshi* presented in Chapter 3 examines this relationship more closely, as well as the homology of this dilambdodont morphology between specimens like UALVP 2846 and on upper molars referred to *Peratherium*.

Many more researchers have discussed phylogenetic relationships between *Alphadon* s.l. and *Peradectes*. *Peradectes* has been considered to be the most closely related taxon to *Alphadon* s.l., with this relationship being expressed either in terms of an ancestor-descendant relationship, or more appropriately, in terms of a sister group relationship (McGrew, 1939; Clemens, 1961, 1966, 1968, 1977, 1984; Turnbull, 1971; Clemens, 1979; Bown and Rose, 1979; Crochet, 1979, 1980, 1984; Fox, 1983; Johnston and Fox, 1984; Sloan, 1987; Reig et al., 1985, 1987; Marshall et al., 1990). Though *Alphadon* s.l. and *Peradectes* have been classified together in the Tribe Peradectini (Crochet, 1979, 1980), the Family Peradectidae (Reig et al., 1985, 1987), and most recently in the Cohort Alphadelphia (Marshall et al., 1990), most authors realize that these higher-level taxa (especially the former two) are paraphyletic, that is, containing the common ancestor but not all descendants of this ancestor (i.e. not including taxa classified in the Tribe Didelphini or the Family Didelphidae). The shared character states given by Crochet (1979, 1980) in the diagnosis of the Tribe Peradectini include predilambdodont upper molars (possessing a straight centrocrista), a conical paracone and metacone subequal in height (also Crochet, 1977a), and on the lower molars, a subequal hypoconulid and entoconid connected by a high crest. An examination of the relative heights of the paracone and metacone on upper molars of *Peradectes*, and a comparision to relative heights on upper molars of *Alphadon* s.l. suggest that the paracone and metacone **are not** subequal in *Peradectes*, as discussed below. This examination is important because the character state "subequal paracone and metacone" is a potential synapomorphy for *Peradectes* plus *Alphadon* s.l. since the state in the outgroup taxa (basal eutherians, *Pappotherium*, and the deltatheroidans) is "paracone larger than metacone", and in the other more derived marsupial taxa (i.e., *Peratherium*), the state is "metacone larger than paracone". The other states given in the diagnosis of the Tribe Peradectini are plesiomorphic, and not indicative of any special relationship between *Peradectes* and *Alphadon* s.l. (as a monophyletic group). Some authors have questioned the hypothesized relationship between *Peradectes* and *Alphadon* s.l. (Krishtalka and Stucky, 1983b; Montellano, 1988; Fox, 1989). Krishtalka and Stucky (1983b; also Montellano, 1988) suggested that *Peradectes* and *Peratherium* share certain derived character states not shared by other taxa classified in the Peradectini, including *Alphadon* s.l. These states were 1) a shorter (anteroposteriorly) talonid, relative to the trigonid, and 2) a cristid obliqua that meets the posterior wall of the trigonid labial to the postcristid notch. Krishtalka and Stucky (1983b) removed *Alphadon* s.l. (and *Albertatherium* Fox, 1971) from the Peradectini and suggested that the tribes Peradectini and Didelphini share a sister group relationship to one another, based on the possession of these synapomorphies.

This hypothesis, and the one regarding a relationship between *Alphadon* s.l. and *Peratherium* (Russell, 1975, 1984) are examined further in this analysis through the inclusion of *Peratherium*, a representative member of the Tribe Didelphini. However, one of Krishtalka and Stucky's (1983b) synapomorphies for the Peradectini plus the Didelphini is questioned. This synapomorphy is the shorter talonid relative to the trigonid, which is not considered to be homologous for these two taxa. Again, this evaluation is supported through an examination of the functional relationships between the upper and lower molars for these two taxa, specifically, the relationship between the protocone of the uppers and the talonid basin of the lowers. In occlusion, the talonid of the lower molars comes into contact with the protocone of the upper molars, resulting in wear facets in the trigonid basin and along the anterior and posterior sides of the protocone (Crompton, 1971). These wear facets suggest that the size of the protocone is correlated with the size of the talonid basin (Clemens, 1968; Fox, 1972, 1975, 1980; Archer, 1982b; Kielan-Jaworowska and Nessov, 1990), especially in terms of anteroposterior length, and if the talonid is shorter than the trigonid, then it would be expected that the protocone would be shorter anteroposteriorly as well. While an anteroposteriorly shorter protocone is observed in most species assigned to *Peradectes* (i.e. *Peradectes chesteri* (Krishtalka and Stucky, 1984: fig.3), this is not the case in species referred to *Peratherium* (i.e. *Peratherium comstocki* (Krishtalka and Stucky, 1983b: fig. 2), in which the protocone is clearly longer anteroposteriorly. Krishtalka and Stucky (1983b: 208) also note that for members of the Tribe Didelphini, the protocone is posterolingually expanded. Therefore, one would expect that the talonid basin for the Didelphini would be longer to accomodate this expanded protocone, rather than shorter relative to the trigonid, as in the Peradectini.

A study of the functional relationship between the anterior part of the trigonid of the lowers and the postmetacrista of the upper molars referred to the Didelphini suggests that the talonid is shorter in these forms because the **trigonid** is relatively wider, rather than being associated with a shorter protocone on the upper molars. As the lower molars move past the uppers during the chewing cycle, the paracristid of the lower molars shears past the metacrista of the upper molars (Crompton, 1971: fig.2, also **Figure 7**). In the Didelphini (i.e. *Peratherium comstocki* (Krishtalka and Stucky, 1983a: fig.2) and *Herpetotherium fugax* (Fox, 1983: fig. 2)), the metacrista is well-developed and extended posterolabially, and is longer than the preparacrista on the anterior portion of the molar. If the metacrista is posteriorly extended and longer, it is reasonable to suggest that this would be correlated with a longer paracristid on the lower molars. One way to lengthen the paracristid is to shift the paraconid (which is connected by the paracristid to the protoconid, **Figure 1**) anteriorly (i.e. *Herpetotherium fugax* (Fox, 1983: fig. 2, **Figure 12A**)), which would have the effect of lengthening the trigonid relative to the talonid, and making the talonid appear relatively shorter. This relationship between a labioposteriorly extended metacrista and an anteriorly shifted paraconid is not seen in *Peradectes*. Therefore, the relatively shorter talonid in *Peradectes* can be correlated with an anteroposteriorly shorter protocone, but in *Peratherium* (where the protocone is said to be expanded posterolingually) it is the trigonid that is relatively wider, because of the morphology of the paracristid of the lower molars and the metacrista of the uppers. The state "talonid shorter than trigonid" is not equivalent (or homologous) in the Peradectini and the Didelphini, and cannot be a synapomorphy grouping these two in a more inclusive monophyletic taxon. This character was eventually removed from the data set used in this study, because after some examination, it appeared that the talonid basin was wider than the trigonid in most taxa examined, including those assigned to *Protalphadon* (i.e., *Alphadon creber*), in which the protocone of the upper molars is clearly anteroposteriorly compressed. As well, Krishtalka and Stucky (1983b) did not clearly state which lower molars they were considering using the character "talonid basin narrower than trigonid"; the trigonid itself decreases in length from M1- M3.

The state "cristid obliqua meets the posterior wall of the trigonid labial to the protocristid notch" is considered to be a synapomorphy for the Peradectini plus the Didelphini not possessed by *Alphadon* s.l. (Krishtalka and Stucky, 1983b), and is not refuted by any consideration of functional relationships between upper and lower molar structures, since in both taxa, the position of the lingual portion of the cristid obliqua appears to be related to a reduced paracone (in terms of height) of the upper molars, relative to the height of the metacone. On lower molars of *Alphadon* s.l., the cristid obliqua runs from the hypoconid to a point on the posterior wall of the trigonid that is basal to the protocristid notch. The position of the cristid obliqua on lower molars of *Peradectes* (and members of the Didelphini, **Figure 12A**), and a consideration of the relationships between, 1) the length of this crest and that of the postparacrista (which runs labioposteriorly from the paracone), and 2) the position of the cristid obliqua and the depth of the hypoflexid (the space between the trigonid and talonid in which the paracone fits as the lower molar moves past the upper on the lower molars to occlusion, **Figure 1**) provide additional evidence that the paracone and metacone on upper molars of *Peradectes* are not subequal, or at least not equivalent to the state "subequal" in *Alphadon* s.l.

During the chewing cycle (**Figure 7**), the hypoconid of the lower molars passes between the paracone and metacone of the uppers. Associated with this, the cristid obliqua and the postcristid shear against the crests of the centrocrista, such that the cristid obliqua shears against the postparacrista and the postcristid past the premetacrista. The crests of each of these pairs appear to be of similar length; for example, the cristid obliqua appears to be approximately the same length as the postparacrista, and it could be predicted that changes in one would be associated with changes in the other. If this is the case, then a reduced or shorter paracone would result in a shorter postparacrista, which may be correlated with a shorter cristid obliqua. As well, the length of the cristid obliqua is associated with the size of the hypoflexid, such that a shorter cristid obliqua can be correlated with a smaller or shallower hypoflexid (Archer, 1976b), which in turn can be correlated with a shorter and smaller paracone (such that the lingual base of the paracone does not extend as far lingually as does that of the metacone). These relative changes have been discussed by Archer (1976b), Crompton and Kielan-Jaworowska (1978: 279) and Crompton and Hiiemae (1970: 29). On lower molars of *Alphadon* s.l., the cristid obliqua contacts the posterior wall of the trigonid below the postcristid notch, suggesting that the postparacrista of the upper molars will be longer and the hypoflexid will be deeper, both of which can be associated with a taller and larger paracone.

On lower molars assigned to *Peradectes* (and *Peratherium* and other members of the Tribe Didelphini or Family Didelphidae), the cristid obliqua is shifted labially, so that it meets the posterior wall of the trigonid near the base of the protoconid. On these lower molars, the hypoflexid is shallower, and the cristid obliqua may be shorter. The differences in the lengths of the cristid obliqua on these lower molars could be quantified through measurement, but for now it is broadly stated that the cristid obliqua is shifted labially (from the postcristid notch), and is relatively shorter on lower molars of *Peradectes* and *Peratherium* (relative to the position and length of the cristid obliqua on lower molars of *Alphadon* s.l.), and is correlated on the upper molars with a shorter postparacrista and a shorter or smaller paracone, relative to the metacone. Also, the more labial position of the cristid obliqua results in a shallower hypoflexid, which may also be associated with a relatively smaller paracone. An examination of several upper molars assigned to *Peradectes*, including the paratype of *P. elegans* (AMNH 17369, maxillary fragment preserving M1-4), indicates that the paracone is clearly lower than the metacone. This difference in relative height was recognized by several researchers (Simpson, 1928b; McKenna, 1960; Clemens, 1966; Archibald 1977, 1982 (quoting from a manuscript by

Clemens); Johnston and Fox, 1984), but the original diagnosis of the type species of *Peradectes*, *P. elegans*, stated that the paracone and metacone were subequal (Matthew and Granger, 1921), forming part of the basis for Crochet's (1979, 1980) classification of *Peradectes* and *Alphadon* s.l. in the paraphyletic Tribe Peradectini. A "subequal paracone and metacone" has been noted for various species of *Peradectes* by several authors (Setoguchi, 1973, in Bown, 1979; Lillegraven, 1976; Krishtalka and Stucky, 1983a). However, in addition to actual observations, the more labially positioned cristid obliqua on the lower molars of *Peradectes* suggests that there is a correlation with a relatively lower or smaller paracone on the upper molars, and that the paracone and metacone in *Peradectes* are not "subequal". Even if there is some misinterpretation of the meaning of "subequal" as applied to *Peradectes*, this state cannot be homologous with the state "subequal" in *Alphadon* s.l. On lower molars referred to *Alphadon* s.l., the cristid obliqua is more lingually positioned, suggesting that this crest is longer and the hypoflexid is deeper, correlated with a taller and larger paracone on the upper molars of *Alphadon* s.l. The character state "subequal" is not applied to *Peradectes* in this analysis, and is reserved for the condition observed in *Alphadon* s.l. The state for *Peradectes* is given as "paracone reduced relative to metacone". This analysis suggests that *Peradectes* and *Alphadon* s.l. may not be as closely related as previously thought, since the only potential synapomorphy grouping these two (subequal paracone and metacone) has been rejected through a functional analysis.

Although researchers often discuss the proximity of phylogenetic relationships at the generic level ("*Alphadon* s.l. and *Peradectes* are sister taxa"), character states cannot feasibly be coded and included in PAUP 3.0 for all species assigned to *Peradectes* and *Peratherium* . Ideally, the most basal or most plesiomorphic taxon would be coded, as in the case of the eutherians and australidelphan taxa discussed above. Another option is to code for some general morphology that focuses on invariant characters in the genus, on other words, on characters that occur uniformly throughout the taxon. The first methodology is employed for *Peradectes*, and the second for *Peratherium*. Krishtalka and Stucky (1983b) presented a revised phylogeny for *Peradectes*, suggesting that *P. elegans* (Early Paleocene; Tiffanian-Early Wasatchian) was the most plesiomorphic peradectid, based on dental morphology and its greater stratigraphic age relative to other referred species. The holotype of *P. elegans* (AMNH 17376) includes paired dentaries preserving some premolars and all molars. The paratype (AMNH 17369) is left maxillary fragment with M1-4. Using *Alphadon* s.l. as an outgroup, Krishtalka and Stucky (1983b) suggested that some plesiomorphic character states possessed by *P. elegans* (relative to more derived species of *Peradectes*) included larger molar size, a lower transverse width/anteroposterior length ratio, less of a disparity in this width/length ratio from M1 to M3, stronger stylar cusps and conules, a broad, uncompressed protocone, and lower molar talonids broader than trigonids. More derived peradectids showed a reduction in overall size, an increase in the width/length ratio, and a reduction in the sizes of the stylar cusps, conules and the protocone (also Marshall et al., 1990: 455, **Figure 13A**). Krishtalka and Stucky (1983b) did not distinguish between less and more derived species referred to *Alphadon* s.l., and when discussing the primitive morphology as represented by *Alphadon* s.l., listed a wide range of character states. Recent hypotheses concerning the phylogenetic relationships of species assigned to *Alphadon* s.l. and reconstructions of the morphology of the hypothetical marsupial upper molar (Marshall et al., 1990; Cifelli, 1990a, both reviewed earlier), would produce a different set of character states for the outgroup (*Alphadon* s.l.) from those used by Krishtalka and Stucky (1983b). Since taxa classified in *Protalphadon* are considered to be the most plesiomorphic taxa once referred to *Alphadon* s.l. (Cifelli, 1990a), it would be more appropriate to derive outgroup characters from within *Protalphadon*. These character states would include smaller molars with a greater width/length ratio, a compressed protocone, and reduced stylar cusps C and D and conules, and would result in a reversal of the peradectid phylogeny given by Krishtalka and Stucky (1983b: fig. 6). In this phylogeny, *P. chesteri* and *P. minutus* are two of the more derived taxa, and share the following synapomorphies- greater disparity in length/width ratio from M1 to M3, stylar cusps C and D and conules reduced to absent, M3 wider transversely (greater length/width ratio), with a highly compressed protocone. These states are more similar to those associated with the ancestral marsupial morphotype and with taxa referred to *Protalphadon* by Cifelli (1990a); therefore, *Peradectes chesteri* and *P. minutus* and other more derived taxa on the cladogram of Krishtalka and Stucky (1983b) would instead be the more plesiomorphic taxa, and species like *P. elegans* would be derived in an increase in overall size and in the size of the protocone and the cusps and conules (**Figure 13B**).

However, the phylogenetic reconstruction of the peradectids presented by Krishtalka and Stucky (1983b) receives support from the proposed sister group relationship between *Peradectes* and *Peratherium* (also Montellano, 1986). Though one of the synapomorphies given by Krishtalka and Stucky (1983b), "talonid relatively longer than trigonid", was criticized above, the second, "cristid obliqua meets trigonid wall labially", was supported through a consideration of the functional relationship of the cristid obliqua and upper molar structures for both taxa. A third potential synapomorphy is "paracone reduced relative to the metacone", which is correlated with the morphology of the cristid obliqua. Krishtalka and Stucky (1983b) stated that the paracone and metacone were subequal in *Peradectes*, but this is not supported by examinations of referred specimens nor of the relationship between the position of the cristid obliqua on the lower molars and the height of the paracone on the uppers. The suggestion that the state "paracone reduced relative to the metacone" is a synapomorphy for *Peratherium* and *Peradectes* is from an initial hypothesis of homology, based on a consideration of the similarity in the relative sizes of the paracone and metacone in these two taxa, and functional similarities between the paracone and metacone and associated crests on the lower molars, as described above. If this hypothesis is supported in the final phylogenetic analysis, then additional synapomorphies for *Peradectes* and *Peratherium* could include an increased molar width/length ratio, broader protocone and stronger stylar cusps (**Figure 13A**). In this phylogeny, *Peradectes elegans* would be the most plesiomorphic taxon referred to *Peradectes*, since this species possesses states similar to those thought to be possessed by the most recent common ancestor of *Peradectes* and *Peratherium*. More derived taxa assigned to *Peradectes* would show a reduction in molar size and in the size of stylar cusps, as suggested by Krishtalka and Stucky (1983b). The hypothesis of *Peradectes elegans* as the most plesiomorphic peradectid receives support from the greater age of *P. elegans* relative to other peradectids. The relationship between plesiomorphy or "primitiveness" of taxa, and stratigraphic position has been criticized (Schaeffer et al., 1972; Wiley, 1981) because an older taxon may share a more recent common ancestry with a younger taxon (based on the possession of synapomorphy), than does a taxon lying between the two, in terms of age or relative stratigraphic position. As well, a younger taxon may be more plesiomorphic than older taxa; the position of *Protalphadon lulli* (Lancian), on the final cladogram (**Figure 26**), is an excellent example. In the case of *Peradectes elegans*, a basal position on the cladogram (Krishtalka and Stucky, 1983: fig. 6) is correlated with a basal stratigraphic position (Tiffanian), so that the morphology associated with this species is the one coded for the phylogenetic analysis presented here.

For *Peratherium*, character states will be coded from what are believed to be invariant or "typical" characters for this genus. The most plesiomorphic species assigned to this genus is not sought, primarily because this taxon is badly in need of revision, and there are many species involved, both European and North American (33 and 23 respectively, Crochet, 1969, 1977a, b), with a large number being based on fragmentary mandibles and lower molars. Also, major differences between referred species often involve only relative age and size (Simpson, 1968; Setoguchi, 1973, in Bown, 1979: 54; Green and Martin, 1976; Krishtalka and Stucky, 1983a, b). For example, Krishtalka and Stucky (1983b: 258) note that the Eocene species of *Peratherium* "bear the diagnostic trademarks of the genus at their earliest appearance". Other difficulities involve the fact that some recent revisions have focused on Eocene (Krishtalka and Stucky, 1983a, b) or Oligocene (Korth, in press) species alone. *Peratherium* has recently been classified (Reig et al., 1987; Marshall et al., 1990) in the Subfamily Herpetotheriinae (Family Didelphidae), along with *Amphiperatherium* Filhol, 1879 (Early Eocene- Middle Miocene, Europe) and *Herpetotherium* Cope, 1873a (Early Oligocene- Early Miocene, N. Am.). These three genera are morphologically similar, leading to much taxonomic confusion, particularly with regards to *Peratherium* and *Herpetotherium*. Thorough reviews of this problem are given by Hough (1961) and Korth (in press), and are discussed below in order to determine what species (and more importantly, what molar morphologies) are referable to *Peratherium*.

Cope (1873b) named *Herpetotherium fugax* as the type species of *Herpetotherium*, and later (Cope, 1873c) referred five new species to *Herpetotherium* from the Orellan (White River Formation, Early Oligocene) of Colorado. As Korth (in press) notes, Cope originally believed that species referred to *Herpetotherium* were insectivores, and did not recognize this genus as a marsupial until 1884 (Cope, 1884b). At this time, Cope referred all species of *Herpetotherium* to the then strictly European Genus *Peratherium*, based on morphogical similarities between the North American and European taxa. Most authors accepted Cope's revision of *Herpetotherium*, and referred additional materials and erected new species of *Peratherium* from North America (i.e., *P. titanelix* Matthew, 1903; *P. merriami* Stock and Furlong, 1922; *P. innominatum*, Simpson, 1928; *P. youngi* McGrew, 1937; Scott, 1941; Galbreath, 1953). Later authors, however, began to question Cope's revision of *Herpetotherium*. Scott and Jepsen (1941) suggested that it was highly unlikely that one genus (*Peratherium*) could be represented nearly contemporaneously on two different continents, and that Cope's *Herpetotherium* may have to be retained for the North American species alone. Lavocat (1952, in Hough, 1961), suggested that the North American species assigned to *Peratherium* should be removed from this genus, because while the European species of *Peratherium* possess an inflected angle of the mandible, Cope (1873a) originally described *Peratherium* (=*Herpetotherium*) *fugax* as lacking this angle. Hough (1961) followed Lavocat's suggestion, but noted that the presence or absence of an inflected angle of the mandible was variable among North American species of *Peratherium*, and therefore restricted *Herpetotherium* to the type species, *H. fugax* but retained other North American species in *Peratherium*. Hough's revision was subsequently criticized by Green and Martin (1976), who noted that most North American species referred to *Peratherium* did in fact have mandibles with inflected angles, but that these had generally been broken off (also Russell, 1984). Green and Martin (1976) reestablished the synonomy of *Herpetotherium* with *Peratherium* by again referring all North American species to *Peratherum*. Crochet (1977a, b, 1979, 1980) subsequently separated *Herpetotherium* and *Peratherium* again by removing all North American species formerly assigned to *Peratherium* and restricting these to *Herpetotherium*. *Herpetotherium* was rediagnosed and separated from *Peratherium* on the basis of the following characters: cusp D dominant on the stylar shelf, a less reduced talonid basin on the last lower molar, stylar cusp C is developed "progressivement sur M3" (Crochet, 1977a: 359), but is doubled on the first two upper molars, with the more anterior cusp tending to disappear. In *Peratherium*, stylar cusp B is the dominant cusp on the stylar shelf, and cusp C was said to tend to disappear on M1-M2 and to be reduced on M3. Therefore, *Peratherium* was only known from Europe and *Herpetotherium* only from North America. This referral was not generally accepted (but see Reig et al., 1987: 79); Krishtalka and Stucky (1983a: 207, 1983b, also Simons and Bown, 1984) suggest that the dental characters used by Crochet (1977a, b, 1979) to separate *Herpetotherium* from *Peratherium* were variable within North American taxa referred by Crochet to *Herpetotherium*, and did not provide enough evidence to remove these species from *Peratherium* and place them in a separate taxon. Fox (1983), based on a newly referred specimen of an associated upper and lower dentition from the White River Formation of Wyoming (Orellan, middle Oligocene), showed that *H. fugax* possessed a diprotodont anterior dentition in which the first two lower incisors were recumbent. Fox (1983) said that this was a uniquely derived character separating *H. fugax* from *Peratherium* (in which the lower incisors are polyprotodont, being procumbent rather than recumbent), and that *Herpetotherium* should be restricted to *H. fugax*, at least until other specimens preserving the anterior portions of the dentition are found. This restriction implied that other species removed to *Herpetotherium* by Crochet (1977a, b, 1979, 1980) would be reassigned to *Peratherium*. Krishtalka and Stucky (1983a, b) followed Fox's (1983) suggestion and also revised the North American Eocene species now classified in *Peratherium*.

Most recently, Korth (in press) revised North American Oligocene and Miocene marsupial taxa and re-removed North American species of this age assigned to *Peratherium*, referring them to *Herpetotherium*. Korth's emended diagnosis of *Herpetotherium* is similar in several respects to a discussion of North American Oligocene taxa of Crochet (1980: 219), focusing on the morphology of the stylar cusps B, C and D on M1-M3. On these molars, cusp D is said to be dominant on M1-2, and cusp C is small and may be fused with D, while stylar cusp C dominates on M3-M4, and cusp B is minute or absent on M3. Though not noted by Korth or Crochet (1980), stylar cusp D may be absent on M3. Based on my own examinations of specimens of *H. fugax* from the UALVP (i.e., Fox, 1983: fig. 2) and AMNH collections, and a comparison with figured specimens of Eocene taxa (Krishtalka and Stucky, 1983a, b; Russell, 1984), I believe Korth's revision to be valid. On M1 and M2, of *Herpetotherium* s.s., stylar cusp D predominates, and there may be a small stylar cusp C at the anterolingual base of cusp D. The homologies of this small cusp are difficult to determine, but it is most parsimonious to assume it is homologous to cusp C. On M3, a large stylar cusp C predominates at the deepest part of the ectoflexus, on the labial border of the tooth. This morphology is distinct from specimens referred to Eocene species of *Peratherium* (Krishtalka and Stucky, 1983a, b), on which stylar cusp B is large, but is reduced (relative to the state in *Alphadon* s.l.), approaching the size of cusps C and D on M1-3. All three of these stylar cusps are well developed on M1-3. Korth (in press) does not provide an emended diagnosis for *Peratherium*, but suggests that the North American Eocene species of *Peratherium* listed by Krishtalka and Stucky (1983b) should be retained in *Peratherium*, since these taxa possess a large stylar cusp B on M1-3, and do not have a dominant central stylar cusp, as in *Herpetotherium*.

Therefore *Peratherium*, as used in this phylogenetic analysis, will include those species referred to *Peratherium* by Krishtalka and Stucky (1983a, b). Setoguchi (1975, 1978) discussed morphological features of both the upper and lower molars separating *Peratherium* from other North American Tertiary marsupial taxa. These features included the presence of a dilambdodont tooth pattern on upper molars of *Peratherium*, and a hypoconulid more posteriorly placed relative to the entoconid on the lowers. Setoguchi (1975:263) suggested that the dilambdodont pattern was functionally related to the position of the hypoconulid on the lower molars (also Robinson, 1968). These character states will be discussed further in Chapter 3. Other character states seem to be relatively stable for species assigned to *Peratherium*, including, on the upper molars, a metacone larger than the paracone, stylar cusp A small, all stylar cusps reduced and more subequal in size (relative to the state in *Alphadon* s.l.), posterior stylar shelf well developed and extended posterolabially, anterior shelf narrower on M1-3, ectoflexus shallow, and for the lower molars, lingual portion of cristid obliqua positioned labially and hypoconulid positioned more posterior to entoconid. Other character states coded for *Peratherium* and all other taxa included in this analysis are given in Chapter 4.

CHAPTER 3

TAXONOMIC REVISION

THE ANCESTRAL MARSUPIAL MORPHOTYPE. The concept of the ancestral marsupial morphotype has changed substantially within the last few years (Fox, 1983, 1985, 1987a, b; Fox and Naylor, 1986; Clemens and Lillegraven, 1986; Cifelli, 1990a; Marshall et al., 1990), from morphotypes reconstructed earlier by Simpson (1928b, 1929, 1948) and by Clemens (1966). This morphotype focuses on the upper molars (since upper molars are more informative than lower molars, both taxonomically and systematically), and represents a **hypothetical** taxon possessing what are thought to have been plesiomorphic character states for the Marsupialia as a whole. The hypothetical nature of this morphotype has not always been clearly stated; several researchers have referred to *Alphadon* s.l. as being or representing the "ancestral" marsupial taxon. Since *Alphadon* s.l. has been thought to occupy this basal position relative to the rest of the Marsupialia, any revision of *Alphadon* must include an examination of the development of the ancestral marsupial morphotype.

Simpson (1928b, 1929: 117) stated that the Subfamily Pediomyinae (including *Pediomys* s.l.) was the most primitive marsupial subfamily and represented the structural ancestor of the Family Didelphidae and perhaps the entire order Marsupialia. Further, Simpson (1929: 119) suggested that "[f]rom a study of very numerous Cretaceous didelphid upper molars as well as of a large series of later didelphids from all known horizons, it is apparent that the ancestral didelphid had typically five stylar cusps...". Simpson further described these cusps, with cusp B never well developed, and cusps C and D better developed ridge-like crests paralleling the labial border of the stylar shelf. This description of the stylar cusps most closely resembles *P. elegans*, in which stylar cusps B and C are small but generally present. Simpson's (1928, 1948) hypothesis was that cusps B and C would increase in size and importance on the stylar shelf, as seen in Tertiary didelphids like *Peratherium* (also Clemens, 1966). Fox (1987: 165) noted that Simpson's hypothesis involved the addition of stylar cusps from a pediomyid-like ancestry. This does not seem to be the case, as Simpson (1929) clearly refers to five stylar cusps in the ancestral didelphid (see also Ride, 1964: fig. 3; Clemens, 1979), so that only an increase in the size of these cusps (and concomittantly, the width of the stylar shelf) would occur.

Clemens (1966, 1968) considered molars assigned to species of *Alphadon* s.l. to be representative of an ancestral marsupial morphotype, based upon a comparison to early Cretaceous (Albian) tribosphenic molars from the Trinity Sands at Greenwood Canyon, Texas, described by Patterson (1956). Patterson could not confidently assign these specimens to either marsupial or placental taxa, and instead classified them as "therians of metatherian-eutherian grade". Clemens (1966) compared the upper molars assigned to this grade taxon to those assigned to *A. marshi* and found certain similarities, for example, a wide, bilobed stylar shelf with five stylar cusps, including a large stylar cusp (B or stylocone) labial to and connected to the paracone by a crest, the preparacrista. Also, both possesed a large stylar cusp C. Clemens (1966) believed that *Alphadon* s.l. was a descendant of a taxon possessing a molar morphology similar to that of the "therians of metatherian-eutherian grade", and further that the earliest marsupials possessed an *Alphadon* s.l -like morphology, including wide stylar shelves (also Butler, 1941) and a large stylar cusp B. Clemens (1966: 54) reconstructed a phylogeny in which the "therians of metatherian-eutherian grade" gave rise to *Alphadon* s.l., which in turn gave rise to the Tertiary marsupial *Peradectes*. In this phylogeny, there are no major changes required in the morphology of the stylar shelf. On the other hand, Simpson's (1928, 1929) hypothesis would result in a phylogeny where the "therians of metatherian-eutherian grade" gave rise to some taxon within the Subfamily Pediomyinae (similar to *Pediomys elegans*), with this pediomyid subsequently giving rise to other didelphids. This phylogeny would require a reduction of the stylar shelf and reduction or loss of stylar cusps from the "therians of metatherian-eutherian grade" to the pediomyid taxon, and then a second increase in the shelf and the re-appearance of the lost or reduced stylar cusps, as seen in more derived didelphids. Clemens considered this phylogeny to be unlikely, and suggested instead that a taxon similar to the "therians of metatherian-eutherian grade" and *Alphadon* s.l. represented the ancestral didelphid, with pediomyids instead being derived relative to this ancestral morphology in the reduction of the stylar shelf and cusps.

Clemens' reconstruction of the ancestral marsupial morphotype was accepted for many years, because as Fox (1987a) noted, it accounted for all the available evidence, including the relationship of the early Cretaceous "therians of metatherian-eutherian grade" to later marsupial taxa. Unfortunately, many researchers began to state that *Alphadon* s.l. itself, rather than a taxon possessing a morphology similar to that of *Alphadon* s.l. represented the ancestral marsupial (Clemens, 1968, 1977; McKenna, 1969; Kirsch, 1977; Fox, 1979a, 1983; Marshall, 1987; Szalay, 1982a; Archer, 1976b; Reig et al., 1985, 1987; Aplin and Archer, 1987), such that *Alphadon* s.l. represented the most primitive (or plesiomorphic) marsupial taxon from which all others were derived. It was never stated which species of *Alphadon* s.l. represented this ancestal morphotype; there is a wide range of morphological variation in specimens referred to *Alphadon* s.l. (i.e. **Figure 6**), such that it is unlikely that the genus as a whole represents this morphotype.

Fox (1983, 1985, 1987a, b; Fox and Naylor, 1986) recently discussed a revised ancestral marsupial morphotype, based partly on a newly described species from the Milk River Formation of southern Alberta, *Iqualadelphis lactea*. One major conclusion of Fox's studies was that *Pediomys* is a composite taxon, and that the name *Pediomys* should be restricted to the type species *P. elegans*. Marshall et al. (1990) listed certain synapomorphies that would preserve the monophyly of *Pediomys*, including a reduction of the anterior stylar shelf and a paracone positioned more labially on the occlusal surface relative to the metacone. The status of *Pediomys* will not be examined here; all species referred to *Pediomys*, other than *P. elegans*, will be referred to as "pediomyids" for comparison to *I. lactea*. *Iqualadelphis lactea* was described by Fox (1987a, b) as being closely related to certain "pediomyids", "*P.*" *prokrejcii* Fox, 1979b and "*P.*" *krejcii* Clemens, 1966. Upper molars of *I. lactea* possess a narrow stylar shelf anteriorly and lack a stylar cusp C, as in several "pediomyid" taxa, but also possess a small stylar cusp B, which is generally lacking in these (except for *Pediomys elegans*). Previously, Clemens (1966) had noted that *P. elegans* (assigned to the Lancian NALMA) possessed a full compliment of stylar cusps, with cusps B and C being only moderately reduced in size compared to the condition in other "pediomyids". Clemens (1966: 34) considered this to be a primitive morphological state for the "pediomyids" as a whole, and an intermediate state relative to the the ancestral marsupial morphotype in which cusps B and C were well developed and the stylar shelf was wider anteriorly and posteriorly, and more derived "pediomyids", for which the anterior stylar shelf was narrower and cusps B and C were reduced or absent. These more derived "pediomyids" included "*P.*" *krejcii*, "*P.*" *cooki* and "*P.*" *hatcheri*, described by Clemens (1966) from the Lance Formation (Lancian). Fox (1987a,b) noted that if the *Alphadon* s.l-like morphology represented the ancestral or primitive marsupial morphotype, and *P. elegans* (also Lancian) represented an intermediate form between the *Alphadon* s.l.-like morphology and other derived "pediomyid" taxa, then as yet undiscovered "pediomyids" assignable to earlier Late Cretaceous Land Mammal Ages (Edmontonian, Judithian or Aquilan) should show a progressively more *Alphadon* s.l.-like molar morphology. This morphology would include wider stylar shelves and less reduced stylar cusps B and C relative to the Lancian "pediomyids".

Sahni (1972) and Fox (1979) described "pediomyid" taxa from the Judith River (Montana) and Oldman (Southern Alberta) formations respectively, with these formations considered as coeval (Russell, 1970; McLean, 1971, 1977; Fox, 1987b). Upper molars assigned to *"Pediomys" clemensi* Sahni 1972 and *"P." prokrejcii* are referable to the Judithian NALMA, and are older than the "pediomyids" described by Clemens (1966). *"Pediomys" clemensi* and *"P." prokrejcii* **did not** possess a more *Alphadon* s.l.-like morphology, showing instead a distinctly pediomyid reduction of the stylar shelf, stylar cusp B, and an absence of stylar cusp C. Fox (1987a, b) noted however, that specimens from the Milk River Formation (Aquilan NALMA) did show a more primitive morphology relative to the Judithian and Lancian "pediomyids", including the presence of a small but prominent stylar cusp B. Stylar cusp C was also absent on these specimens. Fox (1987a, b) suggested that certain specimens from the Milk River Formation (including *Iqualadelphis lactea*) represented early members of three separate lineages within *Pediomys*, and that the reduction of stylar cusp B in these three lineages, from the Milk River specimens to the more derived Judithian and Lancian forms did not involve *Pediomys elegans*, the intermediate "pediomyid" taxon (Clemens, 1966), in which cusps B and C are present. If *P. elegans* did represent an intermediate morphological stage, this would involve the appearance of cusp C from the Milk River specimens (lacking cusp C) to *P. elegans*, and then a loss of cusp C from *P. elegans* to the Judithan and Lancian pediomyids. A more parsimonious hypothesis is that the reduction of stylar cusp B in the "pediomyids" did not pass through a *P. elegans*-like stage in which stylar cusp C was present on the upper molars. Fox (1983, 1985, 1987a, b) also suggested that these "pediomyid" lineages were not related to an ancestral marsupial having five stylar cusps (the *Alphadon* s.l. or *Alphadon* s.l.-like morphology), and that instead, the ancestral marsupial may have lacked stylar cusp C (also Clemens, 1979), with this cusp being added later in marsupial phylogeny. This new hypothesis had important implications for *Alphadon* s.l., because it suggested that an *Alphadon* s.l.-like morphology was not representative of the ancestral morphology, since most species referred to *Alphadon* s.l. possess a stylar cusp C. The absence of stylar cusp C on the ancestral marsupial morphotype is said to be supported by an outgroup comparison to closely related Late Cretaceous eutherians which also show upper molars with distinct cusps B and D but no cusp C (Fox, 1987b), for example *Kennalestes* and *Asioryctes*. It is also supported by an outgroup comparison to the Deltatheroida, and *Pappotherium*, two taxa included as outgroup taxa in the upcoming phylogenetic analysis.

Fox's suggestion that the ancestral marsupial morphotype lacked stylar cusp C has been accepted by the majority of recent workers (Clemens and Lillegraven, 1986; Marshall et al., 1990; Cifelli, 1990a; see Eaton, 1990 for a dissenting opinion), and the presence or absence of stylar cusp C has become particularly important in recent revisions of *Alphadon* s.l. presented by Cifelli (1990a) and Marshall et al. (1990). These studies and the importance of stylar cusp C will be discussed later in this chapter, in conjunction with a revision of *A. creber*.

THE TAXONOMIC STATUS OF SEVERAL SPECIES REFERRED TO *ALPHADON* S.L.

Alphadon s.l. is used in this study to refer to all species referred to *Alphadon* prior to the work of Cifelli (1990a). Cifelli (1990a) presented a revision of *Alphadon* s.l. in which this taxon was separated into two new genera, *Protalphadon*, *Turgidodon*, and a more restricted *Alphadon* (designated here as *Alphadon* sensu stricto). Cifelli's classification was an advance over previous classifications of *Alphadon* s.l. in that it attempted to account for the morphological variation seen in referred species (for example, compare upper molars of *A. rhaister* with *A. creber*, **Figure 6A, B**). However, Cifelli's revision is incomplete because *Alphadon* s.s. was not rediagnosed, and presumably, this taxon included species not referred to either *Protalphadon* or *Turgidodon*. Taxonomic revisions of certain species assigned to *Alphadon* s.l. follow (including a consideration of the new species referred to *Protalphadon* and *Turgidodon* by Cifelli (1990a)), and the status of *Protalphadon*, *Turgidodon* and *Alphadon* s.s will be briefly examined. A further evaluation of these three genera will be presented in Chapter 5, following a discussion of the phylogenetic analysis in Chapter 4. Therefore, though a species may be discussed in this chapter with regards to a certain genus (i.e., *Alphadon creber*), the results of the phylogenetic analysis may suggest an entirely new generic assignment. This method (though longer and less succinct), seems to be appropriate in a work like this one; species are revised, then these revised species are included in the phylogenetic analysis, then the results of this analysis indicates the relationships of these taxa to one another, which in turn may suggest changes in the generic level classification. Therefore, the generic assignments used in Chapter 3 will generally follow those given by Cifelli (*Protalphadon*, *Turgidodon* and *Alphadon* s.s.) for simplicity . At this point it is noted that certain species assigned to *Protalphadon*, for example, *P. lulli*, possess a paracone that is taller than and of equal width to the metacone (Clemens, 1966). Other assigned species, like *Protalphadon creber*, possess upper molars with a paracone subequal in height to the metacone with metacone that is wider than the paracone, similar to the state in other species referred to *Turgidodon* and *Alphadon* s.s. Therefore, *Alphadon creber* is removed from *Protalphadon* in the discussion and revision below.

***ALPHADON CREBER*, AND OTHER SPECIES REFERRED TO *PROTALPHADON*.** Upper and lower molar specimens referred to *Alphadon creber* were originally collected from the Milk River Formation of Southern Alberta (Fox, 1971). These materials represent some of the oldest specimens referred to *Alphadon* s.l., early Campanian in age, and are assigned to the Aquilan NALMA (Lillegraven and McKenna, 1986; Lillegraven and Ostresh, 1990). Fox's (1971: 147) diagnosis of *A. creber* is short; "A small species of *Alphadon*, resembling *A. wilsoni* Lillegraven 1969; upper molars with large stylar cusp B and smaller but well developed cusp D; stylar cusp C mostly absent.". Fox's (ibid.) original description of *A. creber* is more informative, and includes the following-

> " ... (1) cusp C is usually absent, but on some specimens a small cuspule is present on the anterior margin of the middle cleft, behind cusp B, or on the posterior margin, in front of cusp D; (2) the paracone and metacone are separated by a more narrow valley; (3) anteriorposterior lengths are usually less, especially for M1; (4) the protocone is usually less broad, particularly on M1; (5) the posterolabial lobe of the stylar shelf can be larger and the labial border of the crown more oblique in relation to a line through the paracone and metacone, especially on M3."

Fox (1971) originally suggested that specimens referred to *A. creber* can be divided into two morphological types. The first of these consists of upper molars that are (1) slightly smaller, (2) with the labial margin of the stylar shelf being more parallel to a line through the paracone and the metacone, (3) a stylocone that is situated further from the paracone, (4) a notched preparacrista, and (5) a relatively smaller stylar cusp D. In the second morphology, these molars are (1) larger, (2) with a more oblique labial margin, (3) a stylocone that is larger and closer to the paracone, (4) a preparacrista that is unnotched, and (5) a larger cusp D. The second and third characters are associated with the transverse width of the anterior stylar shelf relative to the posterior shelf, and will be the focus of the revision of *A. creber* presented below.

Though Fox (1971) did not specifically refer to stylar cusp C in discussing the two morphologies of specimens assigned to *Alphadon creber*, other recent revisions of this species have focused on the presence or absence of this cusp. These revisions correspond in large part to recent changes in the concept of the ancestral marsupial, as represented by the morphology of the upper and lower molars (Fox, 1983, 1985, 1987a, b; Clemens and Lillegraven, 1986; Cifelli, 1990a; Marshall et al., 1990), including whether or not the upper molars associated with this morphology possessed a stylar cusp C. Fox (1971) originally suggested a morphological and size similarity of *A. creber* to molars referred to *A. wilsoni*, as well as a similarity to "*A.*" *lulli*, based on the variable presence of stylar cusp C (Clemens, 1966). At the time of Fox's original study, the ancestral marsupial taxon was thought to have been characterized by upper molars on which there was a full compliment of stylar cusps, including stylar cusp C, similar to the condition seen in *Alphadon* s.l. (Clemens, 1966, 1968). With this hypothesis, *Alphadon creber*, in which stylar cusp C is only variably present, would be derived relative to the ancestral marsupial morphotype in which stylar cusp C is consistently present. Fox (1971) noted that if it were not for this hypothesis, *A. creber*, known from deposits stratigraphically lower than for any other species referred to *Alphadon* s.l., would make an ideal ancestor to "*A.*" *lulli*. Specimens referred to "*A.*" *lulli* are assigned to the Lancian NALMA (Lance Formation, Clemens 1966, 1973; Hell Creek Formation, Archibald, 1977, 1982) and possibly to the Judithian NALMA ("Mesaverde" Formation, Lillegraven and McKenna, 1986). As discussed at the beginning of this chapter, Fox (1983, 1985, 1987a, b; Fox and Naylor, 1986, based on an original suggestion by Clemens, 1979) recently suggested that stylar cusp C was lacking on upper molars of the ancestral marsupial morphotype, and that *Alphadon* s.l., or an *Alphadon* -like morphology did not represent this ancestral morphotype. At the present time, upper molars of the ancestral morphotype are thought to lack stylar cusp C, but cusps B and D are well developed. The upper molars are relatively wider compared to anteroposterior length, with a more anteroposteriorly compressed protocone and a more closely appressed paracone and metacone. These latter two cusps are high and sharp, with the paracone taller than the metacone (Clemens and Lillegraven, 1986, supported by outgroup comparison with the Deltatheroida), and the centrocrista connecting them is straight. As well, the stylar shelf is wide anteriorly and posteriorly, and the ectoflexus is deep (Marshall et al., 1990).

This revised morphotype, particularly the absence of stylar cusp C, has had important implications for the taxonomic status of *A. creber*, in which some referred upper molar specimens possess a stylar cusp C, while others lack this cusp. Two recent papers have presented different revisions of *A. creber* and have reconsidered the relationships of this taxon to the remainder of *Alphadon* s.l. In the first of these, Cifelli (1990a) erected the new genus *Protalphadon* to include *Alphadon lulli*, *A. creber*, and a new species from the

Kaiparowits Formation (Utah, Judithian), *P. wahweapensis*. Cifelli (1990b) also referred *P. crebreforme* (Wahweap Formation, Utah, Aquilan) to this genus. Cifelli (1990a) diagnosed and described *Protalphadon* on the basis of plesiomorphic character states relative to the remainder of *Alphadon* s.l., and to the Marsupialia as a whole (also Marshall et al., 1990). With regards to the upper molars, these character states included a smaller overall molar size, a higher upper molar transverse width to anteroposterior length ratio, a closely appressed paracone and metacone, and an anteroposteriorly compressed protocone. As well, Cifelli suggested that species classified in *Protalphadon* were characterized by the variable presence of stylar cusp C, as opposed to other species referred to *Alphadon* s.l., in which cusp C was more frequently present. Cifelli (1990a: 316) recognized the problems involved in diagnosing *Protalphadon* on the basis of plesiomorphic rather than synapomorphic character states, but noted that this procedure allowed *Alphadon* s.s. (and *Turgidodon*) to be described on the basis of shared, derived characters, including a larger and consistently present cusp C. Cifelli (1990a: 299) recognized that specimens assigned to *A. creber* may actually be referable to two separate species, based on the earlier suggestion from Fox (1971), but chose to retain the hypodigm in one taxon.

In the second, nearly contemporaneous paper, Marshall et al. (1990) referred upper molar specimens assigned to *A. creber* to two different taxa on the basis of the presence or absence of stylar cusp C and the size of the trigon basin (described as the ratio of the distance from the metacone to the protocone to the anterior width of the molar, M-P/AW). Specimens lacking cusp C and with a higher M-P/AW ratio (the trigon was transversely wider, but more anteroposteriorly compressed) were referred to an informal taxon, *A. creber* [-C]. This taxon was removed from *Alphadon* s.l. entirely by Marshall et al. (1990), and placed in the taxon Peradectoidea *incertae sedis*, within the new taxa Order Peradectia and Cohort Alphadelphia (comparable to the cohorts Ameridelphia and Australadelphia, Szalay, 1982). Other plesiomorphic states noted for *A. creber* [-C] were the parallel position of the paracone and metacone on the occlusal surface, the greater upper molar width to length ratio, a small and spirelike protocone, and a deep ectoflexus (Marshall et al., 1990: 449). These authors suggested that *A. creber* [-C] represented the plesiomorphic marsupial morphotype, and was basal to the late Cretaceous radiation of marsupials. The remaining specimens originally referred to *A. creber* possessed a small but distinct stylar cusp C and had a lower M-P/AW ratio (the trigon was relatively shorter transversely and anteroposteriorly longer) in comparison to *A. creber* [-C]. These specimens were referred to a second informal taxon, *Alphadon creber* [+C]. Marshall et al. (1990) note that *A. creber* [+C] shared several plesiomorphic states with *A. creber* [-C], as listed above.

Marshall et al. (1990) restricted *Alphadon* to all other species previously referred to this genus, possessing derived character states lacking in both *A. creber* [-C] and *A. creber* [+C]. This *Alphadon* s.s. and *Albertatherium* were classified by Marshall et al. (1990) in the new Subfamily Alphadontinae. Further, Marshall et al. (1990) stated that *Alphadon* s.l., as previously conceived, was a polyphyletic taxon, composed of three separate lineages, including *A. creber* [-C], *A. creber* [+C] and *Alphadon* s.s. They noted that this polyphyly can be resolved by removing the former two lineages from *Alphadon* s.l. While this line of reasoning could be accepted for *A. creber* [-C], it is difficult to understand why Marshall et al. (1990) have separated *A. creber* [+C] from *Alphadon* s.s. *Alphadon creber* [+C] possesses a stylar cusp C, and by describing this taxon as a second lineage within a polyphyletic taxon *Alphadon*, they suggest that this stylar cusp appears convergently in *A. creber* [+C] and in their *Alphadon* s.s. There is no evidence to support this hypothesis of convergence, and instead the presence of this cusp is more likely homologous in the two taxa. This homology suggests that *A. creber* [+C] would not be removed from *Alphadon* s.s. Further, Marshall et al. (1990: 480) remove *A. creber* [+C] from the Subfamily Alphadontinae and classify it instead in the Subfamily Peradectinae. This assignment of *A. creber* [+C] to the Peradectinae is confusing, as Marshall et al. (1990: 451) note that *A. creber* [+C] would be an appropriate structural ancestor for *Peradectes* (Subfamily Peradectinae), as well as *Alphadon* s.s and *Albertatherium* (Subfamily Alphadontinae), but by assigning *A. creber* [+C] to the Subfamily Peradectinae, Marshall et al. (1990) imply that this species is ancestral to *Peradectes* and other species classified in the Subfamily Peradectinae alone.

The presence or absence of stylar cusp C has become a very important character in determining the phylogenetic relationships of species referred to *Alphadon* s.l., as is apparent in the revisions of *A. creber* (Marshall et al., 1990) and *Protalphadon* (Cifelli, 1990a). A re-examination of the original hypodigm of *A. creber*, as well as a consideration of other previously unreferred specimens from the upper Milk River Formation assigned below to *A. creber* suggests that it is inappropriate to divide this species on the basis of the presence or absence of stylar cusp C, and instead, a revision of this species must be based on other characters, including those listed in the original description of *A. creber* and discussed by Fox (1971), and others used by Marshall et al. (ibid.). These characters include the relative widths of the anterior and posterior stylar shelves, the width/length ratio of the upper molar, the size of the trigon basin (Marshall et al., 1990), the anteroposterior length of the protocone, and the morphology of the ectoflexus.

Fox (1971: 147) noted that for M1s referred to *A. creber*, the anteroposterior lengths were lower (i.e., the transverse width/anteroposterior length ratio was higher), and the protocone was more anteroposteriorly compressed. As well, the posterior stylar shelf was larger and the labial border more oblique (the anterior stylar shelf is narrower and less well developed), on M1s, M2s and certain M3s. As well, several molars referred to *A. creber*, particularly the M1s, possess a broad and deep ectoflexus, which can be associated with the relative widths of the stylar shelves. General morphological trends observed on upper molars referred to *Alphadon* s.l. include an increase in the depth of the ectoflexus from being shallow and open on M1, to being deeper on M2, and deepest and narrowest on M3 (**Figure 8**). This is related to the trend in the increase in the width of the anterior stylar shelf from narrower on M1, increasing in width on M2, to being equal or subequal in width to the posterior shelf on M3. Also, the protocone becomes anteroposteriorly shorter but transversely wider on M1 through to M3, such that the protocones of M1 and M2 are relatively broader, but narrower transversely. The shortening and widening of the protocone is associated with an increasing molar width to length ratio from M1 to M3.

The anteroposteriorly compressed protocone and the broad but deep ectoflexus seen on M1s and M2s referred to *A. creber* are unusual when compared to trends noted on upper molars of most other species referred to *Alphadon* s.l. With regards to M3s originally referred to *Alphadon creber*, Fox (1971) noted that on some specimens the anterior and posterior shelves were equal in width, while on others, the anterior shelf was narrower. Again, the general trend in molar morphology for *Alphadon* s.l. is an increase in the width on the anterior stylar shelf from M1 through to M3 such that the two shelves are subequal in width on M3. As discussed below, only one of these M3 morphologies is considered to be more in keeping with the morphological trends seen on M1s and M2s in the original hypodigm of *A. creber*. The second group of M3s (which includes the holotype of *A. creber*, UALVP 5545), does not appear to follow these trends, which has important implications in the revision of *A. creber* presented below.

The presence or absence stylar cusp C does not figure prominently in this revision of *Alphadon creber* because cusp C is variably present on the M1s and M2s possessing the distinctive morphology described above (relative to most other species assigned to *Alphadon* s.l.), as is the case with many of the newly referred upper molar specimens from the Milk River Formation. Since most of these specimens are characterized by a distinctive upper molar morphology in the size of the protocone, relative development of the stylar shelves, and depth of the ectoflexus, it may be inappropriate to separate specimens into *A. creber* [-C] and *A. creber* [+C] simply on the basis of the presence or absence of a stylar cusp C. Rather, the presence or absence of a stylar cusp C in *A. creber* may be accounted for by individual variation, as suggested by Fox (1971) and Cifelli (1990a). Some support for this interpretion comes from a consideration of the state of stylar cusp C in "*A.*" *lulli*. Cifelli (1990a) classifed this species in *Protalphadon* along with *A. creber*, partially on the basis of the variable presence of cusp C on upper molars of "*A.*" *lulli*. The revision of *A. creber* presented by Marshall et al. (1990), and their interpretation regarding the presence and/or absence of stylar cusp C in *A. creber* is incomplete in that they did not also consider the variable presence of stylar cusp C within "*A.*" *lulli*. Clemens (1966) notes that only 4 of 21 specimens referred to "*A.*" *lulli* lack a stylar cusp C, but these specimens would have to be referred to "*A.*" *lulli* [-C] for consistency with the revision of *A. creber* given by Marshall et al. (1990). Then, with regards to the phylogeny proposed by Marshall et al. (1990), the relationships of "*A.*" *lulli* [-C] and "*A.*" *lulli* [+C] to *A. creber* [-C], *A. creber* [+C] and *Alphadon* s.s. would have to be determined. Any argument that "*A.*" *lulli* can be characterized by the presence of a small stylar cusp C since only a small percentage of specimens referred to "*A.*" *lulli* lack this cusp (4/21 is 19% of the total number of specimens, compared to 8/15 = 53% for specimens originally assigned to *A. creber*) is invalid because of the small number of specimens available for examination from both species.

It is more appropriate to consider the variable presence of stylar cusp C in both *A. creber* and *P. lulli* as the result of intraspecific variation, as suggested by Fox (1971) and Cifelli (1990a). That the variable presence of stylar cusp C is accounted for by individual variation is supported by a consideration of the functional role of stylar cusp C on the upper molars of *Alphadon* s.l. Clemens (1979: 201) noted that "**[e]xcept where they are minute** (emphasis added), intraspecific variation in the development of cusps in the C and D positions is not exceptionally greater than that of other elements of the crown (also Clemens, 1979: 215)." In other words, when cusps C and D are smaller, intraspecific variation of these cusps is potentially greater. Stylar cusp C was described as a small cuspule, when present, for specimens referred to *A. creber* (Fox, 1971; Cifelli, 1990a). Taking into consideration the quote from Clemens (1979) above, the small size of cusp C within *A. creber* may be associated with intraspecific variation in this taxon, and in "*A.*" *lulli*, relative to other morphological features of the occlusal surface. This is because the small size of stylar cusp C may preclude any function of this cusp during the chewing cycle. What is important to consider here is that the lack of function of a morphological feature reduces the constraints on its evolution. In other words, a feature lacking any function does not become fixed within the population, and instead shows variation, being present in some individuals, but not others.

The functional role of stylar cusp C is difficult to determine because it is not associated with any crest on the occlusal surface, as are most other cusps on upper and lower molar surfaces. These other crests and cusps function as shearing and crushing surfaces during occlusion, producing recognizable and consistent patterns of wear on the upper and lower molars (Crompton, 1971). These patterns of wear provide evidence regarding the functional relationships between cusps and crests on upper and lower molars. Crompton and Hiiemae (1969, 1970) studied dental function in the North American opossum *Didelphis virginiana*, and noted that wear patterns on the stylar cusps suggests cusps C and D acted to puncture food during the initial stages of mastication, but did not occlude with any structure on the lower molars (also Archer, 1976b; Clemens, 1979). Besides puncturing food during mastication, stylar cusp C has been thought to act as a labial block or fence to prevent food being chewed from slipping out between the teeth, or as a guide for the lower molar hypoconid as the upper and lower molars are brought into occlusion (Clemens, 1979). This may be true on upper molars in which cusp C is large, but less so on upper molars where cusp C is reduced. As Clemens and Lillegraven note (1986: 78)-

> "Because stylar cusps C and D of early tribosphenic therians did not occlude with the lower molars, functional constraints on their evolution might not have been as great as on modification of the principle cusps."

Crompton and Hiiemae (1969, 1970) stated that these cusps do not need to occlude with the lower molars to function in mastication, but it is important to note that Clemens and Lillegraven (1986) suggest that the lack of function of morphological features like stylar cusps C and D reduces the constraints on their evolution. Though this suggestion was made with regards to early tribosphenic therians (like the "therians of metatherian-eutherian grade"), in which stylar cusps C and D were smaller, it can be applied to taxa like *A. creber* and "*A.*" *lulli*, in which cusp C is also small or absent on the upper molars. These statements support the hypothesis that presence and absence of stylar cusp C in *A. creber* and "*A.*" *lulli* can be accounted for by individual variation, rather than being taxon-level differences, as was suggested by Marshall et al. (1990). Another morphological feature that shows intraspecific variation is found within species referred to *Turgidodon* (including "*Alphadon*" *russelli* Fox, 1979a, "*A.*" *praesagus* Sahni, 1972, and possibly *A.*

halleyi (Montellano, 1986)) are the protoconal cingula, which lie along the sides of the protocone, basal to the pre- and postprotocrista. These cingula are variably present on referred upper molars, but there has never been any suggestion by workers who have assigned specimens to these taxa (Sahni, 1972; Fox, 1979a; Montellano, 1986; Lillegraven and McKenna, 1986) that the presence or absence of these cingula is accounted for by anything other than interspecific variation in taxa whose referred specimens are otherwise morphologically similar. This variation may be associated with the smaller size of these protoconal cingula (compared to the state in eutherians like *Kennalestes* or *Gypsonictops*), and presumably reduced function in shearing against the lower molars during occlusion in these taxa.

Cifelli (1990a: 315) could not be certain whether the variable presence of cusp C in *Protalphadon*, including *A. creber* (sensu lato) could be explained as a cusp in the process of being reduced, or a cusp in the process of being added, or as some independently acquired variation. To say that stylar cusp C is an independently acquired variation in *A. creber* (and *Alphadon* sp., cf. *A. creber*), and other taxa assigned to *Protalphadon* means that the presence of this cusp would be convergent in *Protalphadon* and in other taxa previously referred to *Alphadon* s.l. This is not supported by the distribution of this character on the final cladogram (**Figure 26**). The suggestion that stylar cusp C is only variably present in *A. creber* and "*A.*" *lulli* for the functional reasons listed above suggests that this cusp is in the process of being added rather than lost, since a large and consistently present cusp C would then be better able to function as a guide for the hypoconid, as a labial block, or in puncturing food. As well, the outgroup taxa used in this study, the Order Deltatheroida, the basal eutherians, and *Pappotherium*, lack a stylar cusp C, so that a cladogram rooted at any of these outgroups would polarize the states associated with stylar cusp C as state 0- C absent; 1- C variably present; 2- C consistently present (**Figure 30A**, character 6). This polarization implies that cusp C is in the process of being added within *Protalphadon*.

A revised diagnosis of *A. creber* is now given, placing more emphasis on characters mentioned in Fox's (1971) description. In the revision given here, specimens previously referred to *A. creber* (and new specimens from the Milk River Formation) are divided into two species, including a more restricted *A. creber*. This restricted *A. creber* is described, but after a new taxon containing a large majority of specimens once assigned to *A. creber*, including most of the M1s and M2s is discussed. These specimens are removed from *A. creber* because of the morphological trends reconstructed from these M1s and

M2s, and extrapolated to the M3 tooth position. Fox (1971) noted that there were two morphologies of M3s assigned to *A. creber*. On the holotype of *A. creber* (UALVP 5545), an M3, and most other M3s in the hypodigm, the anterior and posterior stylar shelves are subequal in width. On other M3s in the hypodigm, the anterior stylar shelf is narrower than the posterior shelf, and the ectoflexus is deeper and broader. As discussed below, this latter morphology appears to be more in keeping with the morphological trends observed on the M1s and M2s previously referred to the hypodigm of *A. creber*. These morphological trends do not include the holotype of *A. creber*, therefore these specimens must be removed from this species. The M3s on which the anterior and posterior stylar shelves are subequal in width, including the holotype, are retained in *A. creber*.

SYSTEMATIC PALEONTOLOGY

Alphadon sp., cf. *A. creber*

Plate 1

Protalphadon wahweapensis Cifelli, 1990a

Holotype. UALVP 5533, M1.

Horizons and localities. The type locality and horizon are UA-MR-6, Upper Milk River Formation, at Verdigris Coulee, Milk River, Alberta (Fox, 1971). Other referred specimens were collected from OMNH localities V6 and V9, lower Kaiparowits Formation, Kane County, Utah (Cifelli, 1990a), and OMNH locality V49, Wahweap Formation, Garfield and Kane Counties, Utah (Cifelli, 1990c).

Distribution. Aquilan and Judithian NALMAS (Campanian).

Referred specimens. UALVP 5533, 5544, 5555, 29520, 29532, 29593, 29517, OMNH 20968 (formerly referred to *Anchistodelphys archibaldi* Cifelli, 1990b), **M1s; 5541, 5558, 29626, OMNH 20115** (type of *P. wahweapensis*), **OMNH 20121 M2s; 5544, 29531, M3s.**

Revised Diagnosis. Differs from *A. creber* and most other species referred to *Alphadon* s.l. in: ratio of transverse width to anteroposterior length greater; protocone low, anteroposteriorly compressed and transversely wider, particularly on M1, M2; anterior stylar shelf narrower than posterior shelf on M1-3, posterior shelf well developed on M1-M3, posterior shelf more posterolabially than labially directed on M1, M2; ectoflexus broader (more open), but deep on M1-M3; differs from other species previously referred to

Alphadon s.l. in: greater molar transverse width/anteroposterior length ratio; stylar cusp C variably present; paracone and metacone closely appressed on occlusal surface, sharp, uninflated; stylar cusps less bulbous and well developed; differs from species referred to *Protalphadon* in: paracone and metacone subequal in height, paracone narrower than metacone in labial view.

Description and Discussion. The first part of this description applies to all three upper molars. Upper molars are small, and transversely wide. All possess a large stylar cusp A that is basally placed relative on the occlusal surface relative to cusp B. Cusp B is the largest on the stylar shelf, is labially positioned relative to the paracone and connected to this cusp by a low preparacrista. A small cusp C may be present posterior to cusp B, but it is absent on several specimens. When present, this cusp is labially positioned, and generally at the deepest part of the ectoflexus. Posterior to C is a larger cusp D, elongate in shape along the labial edge of the stylar shelf, and smaller than cusp B. Cusp E is not present. The paracone and metacone are subequal in height, but the paracone is narrower than the metacone in labial view. These cusps are closely approximated on the occlusal surface, a function of the reduced anteroposterior length of the molar, and are conical and uninflated. The centrocrista is straight and the apex does not extend towards the stylar shelf. The protocone is anteroposteriorly compressed, and transversely wider. There is no basal posterior expansion of the protocone and no protoconular cingula. The conules are well developed, as are the internal cristae.

M1s - The first upper molars have a greater transverse width to anteroposterior length ratio, and an anteroposteriorly compressed protocone. This greater width to length ratio, and the morphology of the protocone are unusual for M1s of *Alphadon* s.l., on which the protocone is usually longer anteroposteriorly and shorter transversely (i.e., **Figure 8**). The anterior stylar shelf is reduced relative to the well developed posterior shelf, and on most specimens referred to *Alphadon* sp., cf. *A. creber*, the postmetacrista is oriented posteriorly. The ectoflexus on these specimens is broad, or more open, but deep, because of the well developed posterior shelf. This morphology is similar to that seen on more typical M1s referred to *Alphadon* s.l., except that on these, the ectoflexus is shallower (compare **Plate 1A - H**, M1s of *Alphadon* sp., cf. *A. creber*, with the M1 in **Figure 8**). The morphology described above for M1s of *Alphadon* sp., cf. *A. creber* is also seen on OMNH 20968, originally designated as an M2 of *Anchistodelphys archibaldi*, but listed above as an M1 of *Alphadon* sp., cf. *A. creber*. In the diagnosis of *A. archibaldi*, Cifelli (1990b:325) notes that stylar cusps C and D are either only slightly developed or absent. On OMNH 20968 (**Plate 1C**), these cusps are clearly present, but are smaller than on other M1s of *A. creber*. The taxonomic weight placed on the presence/absence and sizes of stylar cusps C and D has been criticized above. OMNH 20968 is referred to *Alphadon* sp., cf. *A. creber* because of similarities in the reduced width of the anterior stylar shelf, the well developed posterior shelf, the overall shape of the labial border of the stylar shelf, and the anteroposteriorly compressed protocone. The smaller sizes of the posterior stylar cusps are accounted for by individual variation within this species. Several new upper molar specimens from the Milk River Formation have been referred to *Alphadon* sp., cf. *A. creber*. These specimens possess the morphology described above, and these differ from M1s originally referred to *A. creber* (Fox, 1971; the catalogue numbers of these begin with the numbers "55"), in that stylar cusp C is generally present.

M2s - The morphology of the second upper molars is similar to that of the first upper molars in several respects. The molars themselves are wider than long, and the protocone is low and compressed anteroposteriorly. The anterior shelf is increased in transverse width, and stylar cusp B is further removed from the paracone, but the anterior shelf is still narrower relative to the posterior. The increase in the width of the anterior shelf results in a deeper ectoflexus than on M1, but the ectoflexus is still broader and more open. The postmetacrista is more posteriorly than labially oriented, but it is less posteriorly oriented than on referred M1s. An increase in the molar width, width of the anterior stylar shelf and the depth of the ectoflexus are morphological trends occuring from M1 to M2 and then to M3 of other species of *Alphadon* s.l. (**Figure 8**). As well, the protocone becomes more compressed anteroposteriorly from M1 to M3. Though the second molar increases in width and the protocone is shorter anteroposteriorly relative to the first in *Alphadon* s.l., the change is subtler in *Alphadon* sp., cf. *A. creber* since referred M1s and M2s both show large molar width/length ratios and more compressed protocones. Nevertheless, the similarity in morphology of these M1s and M2s supports their association and referral to *Alphadon* sp., cf. *A. creber*. OMNH 20115, the type specimen of *Protalphadon wahweapensis* (**Plate 1L**), was originally designated as an M3 of this species. In the diagnosis for *P. wahweapensis*, Cifelli (1990a: 299) noted that this species was similar to *A. creber* (sensu lato) in the possession of upper molars showing stylar cusp B more closely appressed to the paracone (i.e., narrower stylar shelf anteriorly), and in a narrower or more anteroposterioly compressed protocone. These character states were said to be diagnostic of *Alphadon* sp., cf. *A. creber* above, and here, OMNH 20115 is designated as an M2 (because of the morphology of the stylar shelf and the protocone) of this species. Cifelli (ibid.) notes that *P. wahweapensis* differed from *A. creber* (sensu lato) on the basis of characters he had listed in the diagnosis for *P. wahweapensis*, but an examination of this diagnosis (ibid.) shows that no such characters were listed. Certain other specimens of *P. wahweapensis* are referred below to *A. creber* s.s., or are considered too poorly preserved for any taxonomic assignment.

M3s- Neither *Alphadon* sp., cf. *A. creber* nor *Alphadon creber* are known from any specimen where M1-3 are associated. This is unfortunate, because trends in molar morphology from M1 through to M3 for both species must instead be reconstructed from isolated teeth that are assigned to these species. This reconstruction is complicated by the assignment of M3s with two different morphologies to *A. creber* by Fox (1971), and must be solved by considering the morphology of the two anterior molars and trends in molar morphology from M1-M3 previously recognized for *Alphadon* s.l.

As noted by Fox (1971), M1s and M2s previously referred to *A. creber* and here assigned to *Alphadon* sp., cf. *A. creber* are anteroposteriorly shorter relative to transverse width and show an anteroposteriorly shortened protocone. The anterior stylar shelf is narrow, but the posterior shelf is well developed. A broadly open, but deeper ectoflexus is present. Given the morphology of M1 and M2 for *Alphadon* sp., cf. *A. creber*, what would the morphology of M3 most likely be? Some evidence comes from more complete specimens assigned to other species of *Alphadon* s.l., and on these, the trend from M1 to M3 is towards a widening of the anterior stylar shelf, a deepening and narrowing of the ectoflexus, a shortening of the protocone, and a widening of the tooth relative to anterior-posterior length. In *Alphadon* sp., cf. *A. creber*, the last two trends are present, but are less distinct because referred M1s and M2s are already transversely wider with shorter protocones. Still, given these morphologies, it could be predicted that referred M3s would show an increased width to length ratio, and a more compressed protocone. Since the anterior shelf was so reduced relative to the posterior shelf on the M1s and M2s, perhaps the anterior shelf on M3 would also be reduced, and not subequal relative to the posterior shelf, as in other species of *Alphadon* s.l., even though an increase in shelf width for M3 would be predicted.

Two morphologies are present on M3s originally referred to *A. creber* s.l. Several characters were given by Fox (1971: 148-149) to differentiate between the two, but the focus here will be on the relative widths of the anterior and posterior stylar shelves. In the first morphology, the anterior stylar shelf is narrower than the posterior, and cusp B is closer to the paracone, while on the second, the shelves are more nearly equal in width, such that stylar cusp B is positioned further from the paracone (Fox, 1971). These molars are all transversely wide with anteroposteriorly compressed protocones. Having established that M1s and M2s of *Alphadon* sp., cf. *A. creber* are 1) transversely wider, 2) have an anteroposteriorly compressed protocone, 3) have narrow anterior stylar shelves and well developed posterior stylar shelves, and 4) a broad but relatively deep ectoflexus, and considering morphological trends from M1-M3 for *Alphadon* s.l. in general, M3s referred to *Alphadon* sp., cf. *A. creber* should be even wider, with a shorter or more compressed protocone, and the width of the anterior stylar shelf should increase, as should the depth of the ectoflexus. Given that the anterior stylar shelves on M1s and M2s referred to *Alphadon* sp., cf. *A. creber* were reduced compared to the posterior shelves, and that the degree of this reduction, and the associated morphology of the stylar shelves of these molars was unusual compared to most other species referred to *Alphadon* s.l., M3s of the first morphology (narrower anterior stylar shelf) are assigned to *Alphadon* sp., cf. *A. creber*, while those of the second morphology (wider anterior stylar shelves) are retained in a more restricted *A. creber*. This second morphology includes the type specimen of *A. creber* (UALVP 5545), and several other M3s, but does not include any M1s or M2s originally included in the hypodigm of this species. It is felt that the morphology of these specimens is unusual compared to other species of *Alphadon* s.l., and does not conform, in terms of trends from M1-M3, as closely to the morphology of specimens like UALVP 5545. This revision results in *A. creber* s.s. being known primarily from M3s, but the morphological variability within *A. creber* s.l. noted by several researchers (Fox, 1971; Marshall et al., 1990; Cifelli, 1990a) has been resolved more satisfactorily than through the use of presence or absence of stylar cusp C, which was criticized above.

Alphadon creber Fox, 1971
Plate 2

Holotype. UALVP 5545, M3.

Horizon and type locality. UA- MR- 6, Upper Milk River Formation, at Verdigris Coulee. Milk River, Alberta (Fox, 1971).

Distribution. Aquilan NALMA (early Campanian).

Referred specimens. **UALVP 29519, OMNH 20587 M1s; 29521, 29533, M2s; 5556, 5557, 5542, 5543, M3s.**

Diagnosis. Differs from *Alphadon* sp., cf. *A. creber* in: anterior stylar shelf equal in width to the posterior shelf on M3; ectoflexus generally deeper and narrower, stylar shelf bilobed, stylar cusp B placed further from paracone on M3; on referred M1s and M2s (none from original hypodigm): ratio of transverse width to anteroposterior length lower, posterior shelf wider than anterior shelf, but not as strongly developed, and not as posteriorly directed as in *Alphadon* sp., cf. *A. creber*; ectoflexus broad but shallower; protocone less anteroposteriorly compressed and transversely shorter. Differs from other taxa previously referred to *Alphadon* s.l., and more specifically from taxa referred to *Protalphadon* in same characters as described for *Alphadon* sp., cf. *A. creber*.

Description and Discussion. UALVP 5556, 5557, 5542, 5543 were referred to *A. creber* by Fox (1971), and are retained in the revised *A. creber* discussed here. These specimens differ from M3s assigned to *Alphadz* sp. cf. *A. creber* in characters listed in the diagnosis. New M1s and M2s from the Milk River Formation are tentatively referred to *A. creber*. On all specimens referred to *A. creber*, the paracone and metacone are subequal in height, sharply conical, uninflated and closely approximated on the occlusal surface. The centrocrista is straight, and not directed towards the stylar shelf. The anterior stylar shelf is equal in width to the posterior shelf. Stylar cusp A is large and positioned basally on the occlusal surface relative to stylar cusp B. Cusp B is the largest cusp on the stylar shelf, labial to and well separated from the paracone. The paracone and stylar cusp B are joined by a long, low preparacrista. Stylar cusp C is either reduced or absent and if present is positioned at the deepest part of the ectoflexus. Stylar cusp D is generally large (but smaller than cusp B) and elongate along the posterior stylar shelf. The ectoflexus is broadly open and shallow on M1 and M2, but deeper and narrower on M3, giving the stylar shelf a bilobed appearance. The protocone is compressed anteroposteriorly and V-shaped, with no basal expansion and no protoconal cingula.The conules are present, well developed, with relatively strong internal cristae.

Fox (1971) described the morphological variation in the M3s originally referred to *A. creber*, and noted that some specimens had a more oblique labial margin of the crown, while on others, this labial margin was more parallel to a line through the tips of the paracone and metacone. These former specimens were removed from *A. creber* and assigned to a new species, *Alphadon* sp., cf. *A. creber*. M3s retained in *A. creber* are otherwise similar to those classified in *Alphadon* sp., cf. *A. creber*. Comparable morphological variation was not recognized for M1s and M2s originally assigned to *A. creber*, these specimens being consistently similar in having a high molar length/width ratio, a compressed protocone, a narrower anterior stylar shelf, and a broad but deeper ectoflexus. M3s classified in *Alphadon* sp., cf. *A. creber* are generally similar to referred M1s and M2s and conform most closely to predicted morphological trends in anterior stylar shelf width on M1-M3.

Two new species are described below. These are assigned to the Genus *Protalphadon*, the composition of which will be discussed further in Chapter 5. As noted earlier, species assigned to *Protalphadon*, including *P. lulli*, are separated from other species retained in *Alphadon* s.l. in certain features of the upper molars, including a paracone taller than the metacone and the subequal size of the paracone and metacone (actually anteroposterior length) in labial view. *Alphadon creber* and *Alphadon* sp., cf. *A. creber* possess a subequal paracone and metacone and a metacone that is larger than the paracone in labial view, and therefore are removed from *Protalphadon*, contrary to Cifelli (1990a). The two new species described below share certain similarities with *P. lulli*, and with certain outgroup taxa (i.e. *Pappotherium*), suggesting that these two new species be retained within *Protalphadon*.

PROTALPHADON n. sp. A

Plate 3

Type specimen. UCMP 109031, RM3.

Referred specimens. UCMP 117696, 117695, ?M3s, all specimens previously referred to "*Alphadon*" *lulli* (Clemens, 1966; Archibald, 1977, 1982). UCMP 47475, jaw fragment with M2-3 also previously assigned to "*A.*" *lulli*, is tentatively referred to this new species.

Horizons and localities. The type locality for this species is UCMP V-73087 (Hell Creek Formation, Maastrichtian), Flat Creek #5, Garfield County, Montana (Archibald, 1977, 1982). Other localities include UCMP V73087, Hell Creek Formation, Montana and UCMP V-5620, Lance Formation, Wyoming (Clemens, 1966).

Distribution. Lancian NALMA.

Diagnosis. Similar to *Protalphadon lulli*, and differing from most other species once referred to *Alphadon* s.l. in:- paracone and metacone of equal width in labial view, postcingulum absent, trigon basin more ventrally positioned relative to apex of centrocrista. Differs from *P. lulli* : paracone not noticeably taller than metacone, stylar cusp C more consistently present; apex of centrocrista rounded, shifted labially towards, but not reaching labial edge of stylar shelf, valley between paracone and metacone deeper, shorter and narrower (measurements as in **Figure 14**, describing depth, length and width of centrocrista, respectively), labial faces of paracone and metacone concave. Differs from *A.*

jasoni Storer, 1991: apex of centrocrista not reaching level of the stylar cusps on the shelf, valley between paracone and metacone narrower, upper molars not dilambdodont.

Description. *Protalphadon* n. sp. A is described here from several M3s. All upper molars have a greater transverse width to length ratio, though this ratio is lower for the M2 than the referred M3s, a common trend on marsupial upper molars. Associated with this width/length ratio, the paracone and metacone are more closely appressed and the protocone is anteroposteriorly compressed. Stylar cusp A is large and ventrally placed, relative to stylar cusp B. Cusp B is the largest stylar cusp, is postioned labial to the paracone, and connected to this cusp by the preparacrista. Stylar cusp C is variably, but more frequently present, and when present is positioned at or just anterior to the deepest part of the ectoflexus. Stylar cusp D is larger than C on the one M2, but is reduced and often as small as cusp C on M3. The anterior stylar shelf is narrower than the posterior on the M2, but both are equally wide on M3. The stylar shelf is wide on referred M3s, such that the bases of the paracone and stylar cusp B do not meet. The ectoflexus is broad on M2, becoming deeper and narrower on M3. On M3, the depth of the ectoflexus gives the stylar shelf a bilobed appearance. The paracone is higher than the metacone on UCMP 109031, but on other specimens, the metacone is nearly of equal height. The paracone and metacone are the same size (width) in labial view, or the paracone is slightly wider. The base of the paracone is more labially placed relative to the base of the metacone, especially on UCMP 47475. The labial faces of these cusps are concave rather than conical. The apex of the centrocrista is directed towards the stylar shelf, in some specimens more so than others. In no specimen does the apex reach the level of the stylar shelf, and this morphology of the centrocrista and the valley between the paracone and metacone is not associated with a dilambdodont condition of the upper molars (this condition is discussed further below, in conjunction with a revision of *A. marshi* and *A. wilsoni*). The conules are well developed, and the anterior cingulum present, running from the paraconule to cusp A, but the posterior cingulum is absent; only a short crest, the postmetaconular crista, running just past the base of the metacone, is present. The trigon basin is deep and more ventrally placed relative to the level of the apex of the centrocrista or the level of the stylar shelf than in other species referred to *Alphadon* s.l., except for *A. jasoni*. The protocone is lower than the paracone and lacks protoconular cingula. UCMP 47475 (referred to "*A.*" *lulli* by Clemens (1966)) is tentatively referred to *Protalphadon* n. sp. A. This specimen is a partial jaw fragment, preserving M2 and M3. The M3 on this specimen is similar to those referred to *Protalphadon* n. sp. A in most features of the diagnosis, except that the centrocrista is not as shifted labially, such that the valley between the paracone and metacone is not as transversely wide. As well, the labial faces of the paracone and metacone of UCMP 47475 are not as concave. The trigon basin is more ventrally or basally shifted relative to the level of the stylar shelf, as in other specimens referred to *Protalphadon* n. sp. A.

Discussion. Even though *Protalphadon* n. sp. A is described on the basis of a small sample size, stylar cusp C is more consistently present than in *P. lulli*, and when present is anterior to the deepest part of the ectoflexus. As well, on upper molars of *Protalphadon* n. sp. A, the trigon basin is low relative to the apex or the deepest part of the V of the centrocrista, and the apex of the centrocrista is slightly directed labially towards the labial edge of the stylar shelf. Certain taxa have upper molars in which the centrocrista is strongly V- shaped, with the apex reaching the level of the stylar cusps. In these taxa, the trigon basin is also displaced basally relative to the level of this apex, so that the walls of the centrocrista are high (the walls of the postparacrista and premetacrista). This morphology is associated with the condition of dilambdodonty, seen in various other marsupial taxa, and eutherian groups such as the insectivorans. Within *Alphadon* s.l., this condition is observed in *A. jasoni*. The apex of the centrocrista is not as strongly displaced in *Protalphadon* n. sp. A, and the valley between the paracone and metacone is transversely narrower, and therefore, the condition of the centrocrista in this new taxon is not associated with dilambdodonty.

Protalphadon n. sp. B
Plate 4

Holotype. OMNH 20120, M3.

Hypodigm. OMNH 20160, M3.

Distribution. Judithian NALMA.

Type Locality. OMNH V6 and V9, Kaiparowits Formation, Utah (Cifelli, 1990a).

Diagnosis. Upper molars transversely wider than anteroposteriorly long, trigon basin wider than long, ectoflexus small and shallow, paracone taller than metacone, similar in size in labial view, base of paracone extends further labially than base of metacone, conules low, placed closer to the protocone than the paracone and metacone.

Description and Discussion. Cifelli (1990a: 297) provided a description of these materials; in addition, stylar cusp A is basally placed on the stylar shelf relative to cusp B, cusp B is largest on the stylar shelf, is sharp and uninflated, and connected to paracone by a low preparacrista. The base of cusp B is positioned closer to base of paracone, suggesting that these teeth are M2s, as originally designated by Cifelli (1990a:

296). As well, the ectoflexus is shallow and small, which is more usual for M1s and M2s referred to *Alphadon* s.l. However, the transverse width/anteroposterior length ratio of the molar and the trigon basin is greater, and the anterior and posterior shelves are almost equal in width, which are more typical of M3s. Because of these latter two features, these specimens are designated as M3s, rather than M2s. Cusp C is absent, cusp D is smaller than B but consistently present. The paracone and metacone are uninflated, conical, and closely positioned on the occlusal surface. The paracone is taller than the metacone, but equal in width, in labial view. The base of the paracone is positioned more lingually relative to the metacone, which is similar to the condition in *Pappotherium* (**Figure 10**). The paraconule and metaconule are as described by Cifelli (1990a: 297), consistently present with weak internal cingula. As well, these conules are positioned closer to the protocone. The protocone is antero-posteriorly compressed.

The description given above is similar to that given by Cifelli (ibid.), except for features mentioned in the diagnosis. Cifelli (ibid.) referred these specimens to *Iqualadelphis lactea*; however, these specimens (OMNH 20120 and 20160) bear little resemblance to those originally referred to *I. lactea* (**Plate 5**) by Fox (1987a). Some of these differences include the following:

1) a larger stylar cusp B (OMNH 20120, 20160) than on the type specimen (UALVP 22823) designated by Fox for *I. lactea*, as well as on UALVP 22824 and 22827.

2) cusp B is positioned labial to the paracone on OMNH 20120 and 20160, but is positioned anterolabially on UALVP 22823 and comparable specimens in the hypodigm (UALVP 22824, 22826, 22827).

3) cusp B is larger than stylar cusp A on OMNH 20120. Cusp B is missing from OMNH 20160, but from the size of the base, appears comparable in size to cusp B on OMNH 20120. Cusp A is larger than cusp B on UALVP 22824 and 22827, but is damaged, but appears larger than B on UALVP 22823. For this reason, cusp B appears larger than A in **Plate 5**, but cusp A is larger, especially when UALVP 22823 is examined in labial view (**Plate 6**).

4) cusps A and B are separated by a strongly notched crest on OMNH 20120 and 20160, but on UALVP 22823, 22824, 22826, and 22827, these two cusps are closely appressed on the stylar shelf, and not separated by a strongly notched crest.

5) cusp B is larger than cusp D on OMNH 20120 and 20160. On UALVP 22823, cusp B is smaller and appears equal in size to cusp D. However, on UALVP 22827, cusp B is broken away, but by the size of its base, may have been larger than D.

6) on OMNH 20120 and 20160, the preparacrista joins the stylocone and the paracone, while on UALVP 22823 and two other specimens in the hypodigm (UALVP 22827, **Plate 5**) the preparacrista runs instead to a point between cusps A and B (contrary to the suggestion of Marshall et al. (1990: 454); the condition on other UALVP specimens is uncertain due to wear).

7) the ectoflexus is smaller, narrower and deeper on OMNH 20120 and 20160, but broader and shallower on UALVP 22823, 22824, 22826, and 22827.

8) the anterior stylar shelf is wider on OMNH 20120 and 20160, so that the anterior and posterior parts of the stylar shelf are approximately equal in width. The anterior stylar shelf of UALVP 22823, 22824, 22826, and 22827 is present but reduced labial to the paracone, similar to the state on more posterior upper molars of several species of "*P*." *prokrejcii*-"*P*." *krejcii* and other "pediomyids".

9) the paracone is noticeably taller that the metacone OMNH 20120 and 20160, while on UALVP 22823, 22824, 22826, and 22827, these cusps are subequal in height.

10) a thin ridge runs from cusp B to cusp D along the edge of the ectoflexus on 22823, 22824, 22826, and 22827 (similar to the state in **Plate 5**, "*P*." *prokrejcii*), but is lacking on OMNH 20120 and 20160.

11) the anterior and posterior cingula are basined on the holotype and specimens of the hypodigm of *I. lactea*, but are flatter and less basined on OMNH 20120 and 20160.

12) on upper molars referred to *I. lactea*, the paracone appears to be shifted slightly labially relative to the metacone. This is especially apparent when the paracone and metacone are seen in labial view. This labial shift was said to be a synapomorphy for the Family Pediomyidae by Marshall et al. (1990: 442, but not noted for *I. lactea*). On OMNH 20120 and 20160, the paracone and metacone are positioned side by side, and the paracone is not shifted labially.

The materials referred to *Iqualadelphis lactea* by Cifelli and those referred to *I. lactea* by Fox do share some similarities, including an upper molar transverse width that is greater than the antero-posterior length, an anteroposteriorly shorter protocone, tall, uninflated paracone, metacone and protocone, and the absence of stylar cusp C, all of which are considered to be plesiomorphic character states for the Marsupialia as a whole (Fox, 1987a, b; Cifelli, 1990a; Marshall et al., 1990). The differences between these specimens strongly suggest that the Kaiparowits specimens be removed from *I. lactea*, and here a new species is erected within *Protalphadon* to accommodate these. The lower molars associated with these upper molar specimens by Cifelli (1990a: 297) are not included in *Protalphadon* n. sp. B because on these lower molars, the cristid obliqua meets the posterior wall of the trigonid at a point basal to the postcristid notch. As discussed earlier, the height and size of the paracone is thought to be functionally correlated with the position of the cristid obliqua at the posterior wall of the trigonid, such that a taller paracone (as in *Protalphadon* n. sp. B) would be correlated with a more lingually positioned cristid obliqua. As well, the more lingual position of the base of the paracone on upper molars of *Protalphadon* n. sp. B could be correlated a larger hypoflexid and a more lingually positioned cristid obliqua. Since this is morphology is not seen on the lower molars originally associated with upper molars here assigned to *Protalphadon* n. sp. B, the lower molars are not included in this new species. A revised diagnosis of *Protalphadon* will be provided in Chapter 5, but it will be noted here that *Protalphadon* n. sp. B shares certain similarities with other species referred to *Protalphadon*, including a paracone taller than the metacone, but with these cusps being equal in size in labial view.

One final species must be considered in this discussion of taxa referred to *Protalphadon*. *Protalphadon crebreforme* Cifelli, 1990b is described from the lower and middle Wahweap formation, Utah (early Campanian, taxa assigned to the Aquilan (Cifelli, 1990b; Lillegraven and Ostresh, 1990) NALMA), on the basis of two damaged upper molars, both lacking the protoconal region. *Protalphadon crebreforme* was said to closely resemble *A. creber* (s.l.), differing in the larger size and greater robustness of stylar cusps and in the greater separation and inflation of the paracone and metacone on the occlusal surface. Cifelli (1990b: 321) notes that on the type specimen, OMNH 20667, the paracone is only slightly larger than the metacone, which shows some apical wear, so that the two cusps were probably originally subequal in height. An examination of a cast of OMNH 20667 suggests that the metacone is only slightly worn apically, and is less worn than the paracone. This is especially apparent in occlusal view (Cifelli, 1990b: fig 2a). The paracone is taller than the metacone in labial view, and since the paracone is more worn than the metacone, the paracone must have been taller before wear occured (the other upper molar specimen, MNA 4561, was not available for examination and is not figured by Cifelli (1990b)).

A paracone taller than the metacone separates *P. lulli* and *Protalphadon* n. sp. A and B from other species once referred to *Alphadon* s.l. (paracone and metacone subequal) and suggests that *P. crebreforme* be retained in *Protalphadon*. However, the type specimen of *P. crebreforme* is anteroposteriorly longer than upper molars referred to *P. lulli* and *Protalphadon* n. sp. A, as indicted by measurements of the paracone to metacone distance (Cifelli, 1990b: 321), and is a more robust tooth. Stylar cusp C is lacking on OMNH 20667 and is said to be present as a small cuspule on MNA V4561, at the deepest part of the ectoflexus and closer to stylar cusp D. Cusp C is variably present in *Protalphadon*, but when present, is at or anterior to the deepest part of the ectoflexus. The centrocrista is straight on OMNH 20667, differing from *Protalphadon* n. sp. A, and the level of the trigon basin relative to the height of the apex of the centrocrista cannot be ascertained since the lingual portion of OMNH 20667 is missing. As well, it cannot be determined whether or not the postcingulum was present. The small number of specimens referred to *P. crebreforme* and their fragmentary nature makes it difficult to assess the relationships of this taxon to others. The taller paracone than metacone suggests that *P. crebreforme* be referred to *Protalphadon*, but *P. crebreforme* lacks or cannot be assessed on the basis of other characters. Cifelli (1990b) suggested a closer relationship with *A. creber*, and if so, *P. crebreforme* would be plesiomorphic relative to *A. creber* (and other species referred to *Alphadon* s.s. and *Turgidodon*) in the possession of a relatively taller paracone. The specimens referred to *P. crebreforme* do not provide enough information to resolve these relationships adequately, and illustrate the problems involved in establishing new species based on a small number of poorly preserved specimens. As such, it is a *nomen dubium*, or a taxon known only from fragmentary specimens. *Protalphadon crebreforme* is removed from *Protalphadon* and is not included in the final phylogenetic analysis.

"*ALPHADON*" *RUSSELLI* FOX, 1979a, "*ALPHADON*" *PRAESAGUS* (RUSSELL, 1952), AND OTHER SPECIES REFERRED TO *TURGIDODON* CIFELLI, 1990. "*Alphadon*" *russelli* and "*A.*" *praesagus* are two species described from the Judith River Formation, Montana (Sahni, 1972; Montellano, 1986), and the Oldman Formation, Alberta (Russell, 1952, Fox, 1979a). "*Alphadon*" *russelli* has also been described from the "Mesaverde" Formation, Wyoming (Lillegraven and McKenna, 1986). These formations are Campanian in age, with "*Alphadon*" *russelli* and "*A.*" *praesagus* being assigned to the Judithian NALMA. "*Alphadon*" *praesagus* was originally described by Russell (1952) as *Delphodon praesagus*, based on a partial dentary preserving a m3 (length and width of this m3 as given by Russell (1952: 113) are 3.3 mm and 2.2 mm, respectively). Sahni (1972) was the first to use the combination "*A.*" *praesagus*, and referred upper and lower molar specimens to this species from the Judith River Formation. The two m3s assigned to this species by Sahni were similar in length, but slightly smaller in terms of width (length = 3.2 and 3.3mm, but trigonid width = 2.0 and 1.8mm), when compared to the holotype of "*A.*" *praesagus*. Sahni (1972: 380) stated that he associated the upper molars from the Judith River Formation to the lowers based on a suggestion of Clemens (1966), that for didelphid marsupials, the lengths of lower molars are generally equal to or greater than the lengths of associated upper molars. Sahni (1972) referred an M1, M2 and a maxillary fragment preserving M3 and M4 to "*A.*" *praesagus*, with lengths and anterior widths of these specimens (taken from available figures) given in **Table 1**. Measurements for referred lower molars (from Sahni, 1972: table 1; "width" is trigonid width) are also given.

Fox (1979) referred new specimens from the Oldman Formation to "*A.*" *praesagus*, and provided a revised diagnosis in which "*A.*" *praesagus* was said to resemble "*A.*" *rhaister*, but to have smaller molar dimensions. Fox (1979: 96) also described a new species from the Oldman Formation, "*A.*" *russelli*, said to be similar to *A. marshi* in size, but having larger posterior premolars, more gracile molars and smaller cusp D on M1-3. Though Fox (1979) compared "*A.*" *praesagus* to "*A.*" *rhaister* and "*A.*" *russelli* to *A. marshi*, he later noted (ibid.: 99) that "*A.*" *praesagus* and "*A.*" *russelli* were morphologically similar, except for "... differ[ences] in size and robustness of teeth, and the sizes of stylar cusps C and D, particularly on M3. The dentition of *A. praesagus* seems more specialized for crushing...". Regarding stylar cusps C and D, cusp C was larger than D on M3s of "*A.*" *russelli* but approximately equal in size to D on M3s of "*A.*" *praesagus* (Fox, 1979a).

Cifelli (1990a), in his discussion of the new Genus *Turgidodon* (to which "*Alphadon*" *praesagus* and "*A.*" *russelli* were assigned), noted that upper molar specimens referred by Sahni (1972) to "*A.*" *praesagus* from the Judith River Formation were more similar in size and morphology of the occlusal surface to those referred by Fox (1979) to "*A.*" *russelli* than to specimens referred by Fox to "*A.*" *praesagus*. Cifelli (ibid.: 302) stated that "...the situation for specimens referred to "*A.*" *praesagus* by Sahni (1972) is less clear-cut. Of the Judith River sample, the upper molars (which are more diagnostic than lowers) all appear referable to *Turgidodon russelli*, differing from *T. praesagus* in being smaller and having less inflated cusps; lower molars are appropriate for either species, but more closely fall within the size range of *T. russelli* ...". Cifelli suggested that Sahni's entire hypodigm of "*A.*" *praesagus* may possibly be referred to "*A.*" *russelli*, so that "*A.*" *praesagus* would not be recognized from the Judith River Formation, instead being restricted to the Oldman Formation of Alberta (consisting of the holotype designated by Russell (1952) and additional specimens assigned to "*A*." *praesagus* by Fox, 1979a).

An examination of upper molars referred by Sahni (1972) to "*Alphadon*" *praesagus* suggests that most of these specimens are indeed more similar to those referred to "*A*." *russelli* by Fox (1979), Lillegraven and McKenna (1986) and Montellano (1986), than to upper molars referred to "*A*." *praesagus* by Fox (1979) from the Oldman Formation. For example, Sahni's specimens are closer in size to those of "*A*." *russelli* than to those referred to "*A*." *praesagus* from the Oldman Formation, and most of the upper molars in Sahni's hypodigm (except AMNH 77344, RM1), have relatively less robust cusps. On the specimens referred by Sahni to "*A*." *praesagus* (ibid., and based on a personal examination) the cusps on the upper and lower molars are large, robust and rounded but not to the extent seen in Fox's Oldman specimens (1979: fig. 1, **Plate 9**), so that the condition of the molar cusps on Sahni's specimens of "*A*." *praesagus* is more similar to that seen in "*A*." *russelli* (Fox, 1979a: fig. 2; Lillegraven and McKenna, 1986: fig. 10; Montellano, 1986).

As well, on M3s referred by Sahni (1972: 379) to "*Alphadon*" *praesagus*, "[s]tylar cusp D is present and is smaller than cusp C.", which is similar to the state observed on M3s (including the M3 on the holotype, UALVP 14805) of "*A*." *russelli* ("stylar cusp C... is usually larger than D... and only occasionally smaller...", Fox, 1979a: 98), on uncatalogued M3s assigned to "*A*." *russelli* in the UALVP collections (**Plate 8**), and the two M3s referred from the Judith River Formation (Montellano, 1986: 97). On the M3 referred to "*A*." *russelli* from the "Mesaverde" Formation, Wyoming (UW 17053, Lillegraven and McKenna, 1986), stylar cusps C and D are said to be small, separate, and approximately the same size. Fox (1979: 94, 98) described the relative sizes of these cusps on the M3s he referred to "*A*." *praesagus* from the Oldman Formation as "...more nearly equal in size, with one or the other being slightly larger in approximately equal frequencies." A reexamination of these specimens and other uncatalogued M3s of "*A*." *praesagus* in the UALVP collections indicates that this is generally the case for all specimens, and also shows that these two cusps are frequently closely approximated and may be joined along their lengths (**Plate 9**). Unfortunately, M3s assigned to "*A*." *praesagus* by Sahni (stored at AMNH) were on loan, and could not be borrowed for photography.

Cifelli's suggestion that upper molars assigned to "*Alphadon*" *praesagus* from the Judith River Formation (Sahni, 1972) are more similar to those of "*A.*" *russelli* from the Oldman, "Mesaverde" and Judith River (those referred by Montellano, 1986) formations, than to molars referred to "*A.*" *praesagus* from the Oldman Formation, is followed here. The taxonomic question to be answered though, is whether Sahni's (1972) hypodigm of "*A.*" *praesagus* from the Judith River Formation should be referred to "*A.*" *russelli*, as suggested by Cifelli (1990a), or whether Sahni's materials have some sort of priority over the morphologically similar specimens referred to "*A.*" *russelli*. In this case, "*A.*" *russelli* would be a junior synonym of "*A.*" *praesagus*. The term "priority" usually refers to taxonomic names, but is used here in the sense that if Sahni's (1972) upper and lower molar materials are considered to be representative of "*A.*" *praesagus*, then these specimens would have "priority" over a later referral of morphologically similar specimens to "*A.*" *russelli*, and these latter specimens should be referred to "*A.*" *praesagus*, rather than Sahni's hypodigm being referred to "*A.*" *russelli* (as suggested by Cifelli, 1990a). If this were the case, then the larger and more bulbous molars referred to "*A.*" *praesagus* by Fox (1979) would have to be removed from this species. If Fox's specimens referred to "*A.*" *praesagus* were considered to be more characteristic of this species, then Sahni's materials would be referable to "*A.*" *russelli*.

Little evidence for solving this problem is provided by a consideration of the holotype of "*Alphadon*" *praesagus*. This specimen is a dentary fragment preserving a m3 of length 3.3 mm and width 2.2 mm. The m3s referred by Sahni to "*A.*" *praesagus* are closely similar in size, as noted above. However, m3s referred by Fox to "*A.*" *praesagus* are also similar in size, with the average for seven specimens being 3.4 mm for length and 2.2 mm for width (Fox, 1979a; table 1). Fox's original unpublished measurements of these specimens show that two m3s have a length of 3.3 mm and widths of around 2.2 mm. The m3s assigned to "*A.*" *russelli* are slightly smaller, the average length and width being 3.0 and 1.8 mm respectively (Fox, 1979a; table 2), though again, Fox's unpublished measurements show that at least one of these m3s is 3.3mm long, and many are over 3.0 mm in length. Upper molars assigned to "*A.*" *praesagus* by Sahni and Fox differ as described in the previous paragraphs, but differences in size between lower molars assigned by both researchers may not be as distinct. Cifelli (1990: 302) noted that lower molars assigned by Sahni to "*A.*" *praesagus* could be assigned to either species, but fall more closely in the size range of "*A.*" *russelli*. Indeed, m1s and m2s referred by Sahni to "*A.*" *praesagus* are more similar in size to m1s and m2s assigned to "*A.*" *russelli* (**Table 1**). It is clear that the holotype of "*A.*" *praesagus* will not be useful in resolving the taxonomic problems, as discussed above. If nothing else, this illustrates the problems caused when taxa are based on isolated lower molars.

There are two morphologies observed within "*Alphadon*" *praesagus*. In the first of these, upper and lower molars are smaller, with less robust cusps, especially on M3. On these M3s, stylar cusp C is usually larger than stylar cusp D. Sizes of m3s in terms of anteroposterior length are lower, but close or equal to the value of the holotype of "*A.*" *praesagus*. In the second morphology, upper and lower molars are larger, with more robust cusps, particularly on M3. Stylar cusps C and D are generally equal in size on M3. On referred m3s, the average lengths and widths are larger than on the holotype of "*A.*" *praesagus*, but certain specimens are equal to the holotype in size. The holotype of "*A.*" *praesagus* is taxonomically uninformative, and cannot answer the question of whether the specimens referred from the Judith River (Sahni, 1972) or the Oldman formations (Fox, 1979a) are more characteristic of this species. Therefore, to resolve these two species, the holotype of "*A.*" *russelli* (UALVP 14805), an upper maxillary fragment preserving P4-M4, should be considered. As discussed above, the M3 on this holotype of "*A.*" *russelli* is similar in terms of size and relative sizes of stylar cusps C and D to M3s referred to "*A.*" *praesagus* by Sahni. Cifelli's original suggestion is accepted, and implemented in a formal taxonomic revision given below. Sahni's hypodigm of "*A.*" *praesagus* is removed and referred to "*A.*" *russelli*. Fox's Oldman specimens are retained in "*A.*" *praesagus*, and this species now corresponds to the usage of all researchers who had subsequently referred materials to "*A.*" *praesagus*. As well, the two new species referred by Cifelli (1990a), *T. madseni* and *T. lillegraveni*, are discussed, as is a new species from the Frenchman Formation, *T. petiminus* Storer, 1991. Again, *Turgidodon* and species assigned to this genus will be discussed further in Chapter 5, in which the evidence for the monophyly of *Turgidodon* is presented in the phylogenetic analysis, and a revised diagnosis of this genus is presented.

Turgidodon russelli (Fox, 1979a)
Plates 7, 8

Holotype. UALVP 14805, maxillary fragment preserving P4-M4.

Referred specimens. See Fox (1979a, including UALVP previously unrecorded UALVP numbers), Sahni (1972), except AMNH 77344, RM1; Lillegraven and McKenna (1986), and Montellano (1986).

Horizon and type locality. Upper Oldman Formation, southeast of Steveville, Alberta.

Known Distribution. Oldman Formation (Fox, 1979a), Judith River Formation, Montana (Sahni, 1972, Montellano, 1986), "Mesaverde" Formation, Wyoming (Lillegraven and McKenna, 1986).

Revised diagnosis. Molars similar to those referred to *Turgididon praesagus*, described below, but differ in: upper and lower molars smaller, with relatively less bulbous cusps; on M3, C, D less robust, stylar cusp C larger than D; cusp C separated from D, on labial edge of stylar shelf and oriented anteroposteriorly; similar to *Turgididon praesagus*, and separated from other species referred to *Turgidodon* and to *Alphadon* s.l. in: stylar cusp C oriented anterolingually-posterolabially away from labial edge of stylar shelf, paralleling orientation of stylar cusp D, especially on M1 and M2; apex of cusp C is "squared" in labial view, not rounded or conical, stylar cusps closely appressed on stylar shelf; bases of stylar cusps closely appressed to bases of paracone and metacone.

Description and Discussion. Materials referred to*Turgidodon russelli* have been adequately described, especially by Fox (1979). The assignment of materials previously referred to *Turgidodon praesagus* (Sahni, 1972) was discussed above. One specimen from this hypodigm, AMNH 77344, and M1, possesses large and bulbous cusps, more so than on other M1s assigned to *T. russelli*. AMNH 77344 is referred below to *T. praesagus*.

Turgidodon praesagus (Russell, 1952)

Plate 9

Holotype. NMC 114, right mandible preserving m3 and the roots of m4.

Hypodigm. includes specimens referred to this genus by Fox (1979), Montellano (1986), also AMNH 77344, RM1.

Horizon and type locality. "Oldman Formation, Belly River Series, Upper Cretaceous; Red Deer River Valley, 4 miles below mouth of Berry Creek, southeast of Steveville, Alberta", (Russell, 1952, also Fox, 1979a).

Known Distribution. upper Oldman Formation, Alberta, Judith River Formation, Montana.

Revised Diagnosis. Similar to *Turgidodon russelli*, differs in larger size of upper and lower molars, greater robustness of cusps, particularly on M3; cusps rounded, inflated, bulbous on upper and lower molars; cusps C and D of same size or C smaller on

M1-3, frequently joined along portion of their heights on M1 and M2; basal expansion of protocone anteriorly, posteriorly and lingually.

Description and Discussion- Beyond differences in molar size and the robustness of the cusps, there are few morphological differences between *Turgidodon praesagus* and *Turgidodon russelli* (compare **Plates 7**, and **8** and **9**). Though it cannot be adequately tested at this time, there is a possibility that the relatively less robust cusps observed on the molars of *T. russelli* may be related to the smaller overall size of the molars referred to this species, relative to the larger molars of *Turgidodon praesagus*. Molar cusps, including the paracone, metacone and stylar cusps do appear somewhat robust and bulbous on individual molars of *T. russelli* (**Plates 7** and **8**), for example, the bases of paracone and metacone often contact the bases of the stylar cusps, and the stylar cusps appear closely appressed on the stylar shelf. Therefore, the bulbousness of the cusps on *T. russelli* may be equivalent to that seen on molars of *Turgidodon praesagus*, once differences in molar size are taken into account. While this suggstion may be true for M1s and M2s, these cusps are clearly less robust on M3s of *T. russelli* (compare **Plates 8** and **9**), including the holotype, UALVP 14805, where M1-3 are associated in one individual (Fox, 1979a; fig. 2c). Because of these distinct differences between the robustness of cusps C and D on the M3s of *T. russelli* and *T. praesagus*, and because the above suggestion regarding the effect of differences in molar size on the relative robustness of the molar cusps cannot be tested yet, the stated differences in the robustness of the cusps in these two species will be accepted, and used to differentiate the two.

Some additional features characterize both of these species and separate them from others referred to *Turgidodon* and to *Alphadon* s.l. For example, cusp C is positioned at the deepest part of ectoflexus on M1-3 and along with cusp D is oriented anterolingually-posterolabially on the stylar shelf of M1 and M2, so that a small shelf or cuspule between cusps B and C is often present. Also, the apex of cusp C is squared in labial view rather than being sharply conical. Some states are shared with *T. rhaister*, and group this species with *T. russelli* and *T. praesagus*, so that these three are more closely related to one another than any are to the remaining species assigned to *Turgidodon* (*T. lillegraveni, T. madseni* and *T. petiminus*). These states include a stylar cusp B strongly inflated labially, and that cusp B, paracone, protocone are subequal in height.

REMAINING TAXA REFERRED TO *TURGIDODON*. *Turgidodon rhaister* is an unusual species assigned to the Lancian NALMA, originally described from the Lance Formation (Wyoming, Clemens, 1966, also Wood and Ormsbee, 1954, originally *Ectoconodon petersoni*), as well as from the Scollard (Alberta, Lillegraven, 1969), and the Hell Creek (Montana, Archibald, 1977, 1982) formations. This species was originally referred to *Alphadon* s.l. by Clemens (1966), and diagnosed as follows (Clemens, 1966:11)- " Molars larger and more bulbous than those of *Alphadon marshi* and *A. lulli*; one or two cusps in C region approximately equidistant from paracone, metacone, and labial margin of shelf; C cusps smaller than B or D; metacone slightly higher than paracone on M1-3; assuming the palate was horizontal, the protocone and paracone are of approximately equal height, in *Alphadon marshi* and *A. lulli*; the protocone is distincly lower than either paracone or metacone." This species was originally referred to *Alphadon* s.l. because on upper molar specimens, cusp A was large and separated from cusp B by a deep notch, and the overall morphology of the shelf was similar to other species of *Alphadon* s.l. Cifelli (1990a) assigned "*A.*" *rhaister* to *Turgidodon*, along with other large and robust species of *Alphadon* s.l. This referral is followed here, since molars referred to *T. rhaister* are the largest assigned to any species once classified in *Alphadon* s.l., and stylar cusps A and B are large and bulbous. Other common features include upper molars with a higher width/length ratio (taken from average values given by Clemens, 1966, M1: 1.07; M2: 1.07; M3: 1.11), an anteroposteriorly longer protocone, the presence of protoconular crista, a shallow trigon basin, and high, wall-like internal conular cristae. *Turgidodon rhaister* can be separated from other species assigned to this genus in the possession of a small stylar cusp C on M1-3, and a less robust cusp D on M2 and M3. These smaller cusps seem unusual on upper molars that are so large and bulbous. As mentioned by Clemens (1966), cusp C is lingually positioned relative to the labial edge of the stylar shelf, and is closely appressed to the posterolabial side of the paracone. This lingual position is not seen on upper molars of any other species previously referred to *Alphadon* s.l.

Turgidodon madseni and *T. lillegraveni* are new species described from the Kaiparowits Formation, Utah. The type of *T. madseni* is a right maxillary fragment, with a fragmentary M1, a well preserved M2 and M3, and the anterolabial corner of M4 (Cifelli, 1990a: fig. 7). Other referred specimens are listed in the hypodigm (Cifelli, 1990a: 306). This species is adequately diagnosed and described by Cifelli (ibid.) and is included in the phylogenetic analysis presented later, with no revision. *Turgidodon madseni* is the smallest and least robust of all species classified in *Turgidodon*; as well, stylar cusp C is larger than D on both M2 and M3, and the ectoflexus is shallow on M2 and M3 (these states cannot be ascertained for the fragmentary M1). The ectoflexus is usually deeper on M3s referred to *Alphadon* s.l. Cifelli (1990a: 307) states that on M1 and M2, the internal conular cristae are faint, but this is not supported by an examination of a cast of the type specimen. These cristae are not as strong as for other species of *Turgidodon*, but still are wall-like and relatively high. The contribution from cusp B to the preparacrista is more strongly developed on *T. madseni* than on other species, and as Cifelli (ibid.: 307) notes, functioned in shearing. Also, the trigon basin is deeper in *T. madseni* than it is for other species referred to *Turgidodon*, and the protocone is more anteroposteriorly compressed. These differences separate *T. madseni* from other species classified in *Turgidodon*.

Turgidodon lillegraveni is not as well diagnosed as *T. madseni*, and additional characters have been recognized through an examination of available casts. Cifelli (1990a: 304) states that *T. lillegraveni* is similar but slightly smaller than *T. praesagus* (Cifelli included specimens referred by Fox, 1979a), with cusps C, D and especially B smaller and lower, and a deeper ectoflexus on M2 than observed for *T. praesagus*. As given in the original description (Cifelli, 1990a: 304), *T. lillegraveni* differs from *T. madseni* and is similar to other species of *Turgidodon* in having a weak preparacrista on the upper molars, including a weaker crest from stylar cusp B, stronger internal conular cristae, and a shallower trigon basin.

***Turgidodon lillegraveni* Cifelli, 1990a**
Plate 10

Holotype. OMNH 20540, right maxillary fragment, preserving M2 and labial half of M3.

Hypodigm. see Cifelli, 1990: 304.

Horizon and known distribution. Lower Kaiparowits Formation, Kane County, Utah (Cifelli, 1990a).

Revised Diagnosis. See Cifelli, 1990a: 304; as well, protocone anteroposteriorly expanded; protoconal cingula variably present (OMNH 20586, fragmentary M2 or M3; OMNH 20589, M3) as in *T. russelli*, *T. praesagus*, *T. rhaister*; differs from other species of *Turgidodon* in- base of paracone larger than base of metacone, apex of paracone shifted labial relative to metacone; paracone wider than metacone in labial view.

Description and Discussion. Cifelli (1990a) described an M4 and upper and lower premolars, and referred upper molars require little additional description. As Cifelli (1990a: 304) notes, the paracone and metacone are subequal in height, but are not equally robust. In occlusal view, the base of the paracone is larger than that of the metacone, implying a more robust paracone. Though this character state was not given in the original diagnosis of *T. lillegraveni*, Cifelli (1990: 304) does mention that in this species, cusp B is "... smaller and lower than in *T. praesagus*, with cusp B more tightly appressed to paracone than in that species...". The proximity of cusp B and the paracone may be associated with the larger base of the paracone in *T. lillegraveni*. In labial view, the paracone is slightly wider than the metacone, contrary to the state in most other taxa referred to *Alphadon* s.l. (except *Protalphadon lulli* and *Protalphadon* n. sp. A, in which these cusps are equal in width), where the metacone is wider than the paracone. The paracone appears to be shifted somewhat labially relative to the metacone. This state is not seen in taxa referred to *Alphadon* s.l., but is observed in "*Pediomys*" (Marshall et al., 1990). The paracone is not as labially shifted on upper molars assigned to *T. lillegraveni* as on those referred to "*Pediomys*", and *T. lillegraveni* is clearly not referable to this taxon. The morphology of the paracone on upper molar specimens referred to *T. lillegraveni* separates this species from others assigned to *Turgidodon*, in other words, the character states associated with this morphology are autapomorphies, and are not included in the phylogenetic analysis presented later. The protocone is anteroposteriorly expanded, the trigon basin is shallow, the internal conular cristae are stronger and wall-like, and protoconal cingula are present, separating *T. lillegraveni* from *T. madseni*, and associating *T. lillegraveni* with the other species assigned to *Turgidodon*. *Turgidodon lillegraveni* lacks the robust cusps C and D (especially on M2, M1 is unknown) seen on upper molars of *T. russelli* and *T. praesagus*.

Two upper molar specimens (OMNH 20117, M2; OMNH 20465, M1) were referred to *Turgidodon* sp. cf. *T. lillegraveni*. Cifelli (1990a: 305) suggested that these specimens were similar in size and most other features to *T. lillegraveni*, but were different in that on OMNH 20117, cusps C and D were lacking, and instead there was a low, linear ridge extending posteriorly from the ectoflexus. If this specimen did belong to *T. lillegraveni*, then this morphology would represent an extreme variant of the stylar shelf. OMNH 20465 (M1) is missing the posterior part of the stylar shelf, and so cannot be adequately compared to OMNH 20117. Cifelli (1990a: 306) notes that OMNH 20465 has robust stylar cusps and is a larger tooth, but is too small to be referred to *T. lillegraveni*. Additionally, the trigon basin on this specimen is deeper than that observed on upper molars of *T. lillegraveni* and the morphology of the paracone is dissimilar. This suggests that OMNH 20465 would not be referable to *T. lillegraveni*. *Turgidodon* sp. cf. *T. lillegraveni* is not included in the upcoming analysis because it is poorly known (based on only two dissimilar specimens) and the morphology of the posterior stylar shelf for OMNH 20117 is not useful in assessing relationships to any other taxa.

A new species of *Turgidodon* has been recently described from the Frenchman Formation (Gryde locality, Maastrichtian, Storer, 1991). Storer (ibid.) originally referred this species to *Alphadon* s.l., but clearly recognized similarities with species referred to *Turgidodon*, based on characters given in the diagnosis and description. These include massive crowns with bulbous cusps, low and rounded stylar cusps, and a shallow trigon basin. Therefore, this species, *T. petiminus*, will be classified in *Turgidodon* for this analysis. Storer (ibid.) suggested that *T. petiminus* was most similar to *T. russelli* in size and that molar specimens referred to both were low-crowned with very shallow occlusal patterns (height of cusps relative to molar surface), and low, bulbous stylar cusps B and D. Molars referred to *Turgidodon rhaister* and *T. praesagus* were said to have deeper occlusal patterns. On upper molars of *T. petiminus*, stylar cusp C is very large, and is labially placed on the stylar shelf, at the deepest part of the ectoflexus. A short but readily distinguishable crest runs lingually from stylar cusp C, particularly on M3, and this feature (not mentioned in the original diagnosis), also serves to separate *T. petiminus* from other species of *Turgidodon*, especially *T. russelli*. Because this character state is an autapomorphy, *T. petiminus* is not included in the final phylogenetic analysis, but is included in the final classification presented in Chapter 5.

TAXONOMIC REVISION OF OTHER SPECIES REFERRED TO *ALPHADON* S.L.

***ALPHADON MARSHI* SIMPSON, 1927 AND *ALPHADON WILSONI* LILLEGRAVEN, 1969.** *Alphadon marshi* Simpson, 1927 and *A. wilsoni* Lillegraven, 1969 are assigned to the Lancian and possibly the Judithian or "Edmontonian" NALMAs (Rigby and Wolberg (1987) described a mammalian fauna from the lowermost Kirtland Shale, New Mexico, including *Alphadon* cf. *wilsoni*, and correlated this fauna with those from the Judith River and Oldman formations (Sahni, 1972; Fox, 1979a). The New Mexico fauna would then be assigned to the Judithian NALMA. Lillegraven and Ostresh (1990) instead assigned this fauna to the "Edmontonian" NALMA). The criteria used to distinguish *A. marshi* and *A. wilsoni* from one another, including molar size and relative sizes of certain stylar cusps (Lillegraven, 1969), have recently been criticized (Fox, 1989). A re-examination of upper molar specimens referred to these two species from various localities across North America, and a consideration of the revised diagnosis for *A. marshi* provided by Clemens (1966) suggests that, 1) there are two distinct upper molar morphologies observed within **both** *A. marshi* and *A. wilsoni* that do not involve molar size or relative sizes of stylar cusps; 2) the first of these morphologies is described most closely in the diagnosis of *A. marshi* (Clemens, 1966), and specimens of *A. marshi* showing this morphology, including the holotype of this species, YPM 13659 (Simpson, 1927, 1929, **Plate 11A**), are assigned below to a restricted *A. marshi* sensu stricto; 3) the type specimen of *A. wilsoni* (UALVP 3681, **Plate 11B**), and parts of the hypodigm possess this upper molar morphology; therefore, *A. wilsoni* is a junior synonym of *A. marshi* s.l.; 4) the second morphology observed within *A. marshi* s.l. and *A. wilsoni* shows similarites to members of the Family Didelphidae (i.e., *Peratherium*) in the shape of the centrocrista and other associated characters. These specimens are referred to *A. jasoni* Storer, 1991, rather than to any taxon classified in the Family Didelphidae; 5) previous definitions and uses of the term "dilambdodonty" are insufficient for distinguishing between the morphology of the centrocrista on upper molars of *A. marshi* s.s. and *A. jasoni* Storer, 1991.

Alphadon marshi was first described from the Lance Formation, Niobrara County, Wyoming by Simpson (1927, 1929) as the type species for *Alphadon* s.l. Simpson (1927) did not provide a satisfactory diagnosis for *A. marshi*, and the type specimen was not figured until 1929. Further work on materials from the Lance Formation was done by Clemens (1961, 1963, 1966, 1973), who provided a revised diagnosis for *Alphadon* and *A. marshi*, and recognized two new species, *A. lulli* and *A. rhaister*. Clemens' (1966: 5) revised diagnosis for *A. marshi* includes the following-

> "...stylar cusp C large and well separated from B, C usually in a central position on the stylar shelf but on a few teeth it is on the labial margin; paracone of same height as or slightly higher than metacone... paracone tends to be more slender than the metacone; paracone and metacone separated by a broad valley that, on most teeth, ends at the lingual side of stylar cusp C."

Clemens (1966: 8) recognized that upper molars assigned by him to *A. marshi* showed a wide range of variation in size measurements, and further that there was some evidence of bimodality in these measurements. Clemens suggested that this bimodality indicated that specimens referred to *A. marshi* might instead be separated into two distinct species, but retained these materials in this species. Lillegraven (1969), working with specimens from the Scollard Formation (Maastrichtian, central Alberta) referable to *A.*

marshi, also recognized a wide range in molar measurements and a bimodality similar to that noted by Clemens (Lillegraven, 1969: figs. 16, 17). Based on this additional evidence, Lillegraven divided *A. marshi* into *A. marshi s.s.* and a new species, *A. wilsoni*. Molars referred to *A. wilsoni* were said to be smaller than those referred to *A. marshi* s.s., although Lillegraven (1969: 39) noted that the upper and lower molars of *A. wilsoni* were proportionately longer, in terms of the ratio of anteroposterior length to transverse width.

Lillegraven listed additional differences between *A. wilsoni* and *A. marshi* in their respective diagnoses, many of which dealt with premolar morphology. Some of these differences included the extent and completeness of the cingulum on P3, and the relative sizes of p2 and p3. Generally though, differences in upper molar morphology are more diagnostic and taxonomically useful than those in the premolars, and will be the focus of this revision. The only upper molar character other than relative size given by Lillegraven to differentiate between *A. wilsoni* and *A. marshi* involved the relative sizes of stylar cusps C and D on M3. As Lillegraven (1969: 42) noted-

> "Disregarding general proportions, the **only consistent morphological difference** [emphasis added] between the upper molars of *A. marshi* and *A. wilsoni* is the fact that in the latter, stylar cusp D is smaller than C in the M3... All the upper Edmonton [now Scollard Formation, Gibson, 1977] specimens of *A. marshi*... have stylar cusp D exceeding the development of C."

Lillegraven's recognition of *A. wilsoni* and separation of this species from *A. marshi* were accepted by subsequent workers, including Clemens (1973). Based on the criteria given by Lillegraven (1969), Clemens (1973) removed certain specimens he had assigned to *A. marshi* from the Lance fauna and referred these to *A. wilsoni*. Other authors have referred materials to *A. wilsoni* (Archibald, 1977, 1982), *Alphadon* cf. *wilsoni* (Rigby and Wolberg, 1987) or *Alphadon* cf. *A. wilsoni* (Flynn, 1986). However, Lillegraven's criteria for separating *A. wilsoni* from *A. marshi* and other species of *Alphadon* have been questioned by Clemens (1973) and Fox (1989).

With regards to the relative sizes of the stylar cusps C and D on M3, Clemens (1973) noted that some specimens of M3s from the type Lance Formation referred to *A. marshi* (on the basis of molar size) possessed a morphology where stylar cusp C was the same size or larger than stylar cusp D, the morphology said by Lillegraven (1969) to be characteristic for M3s of *A. wilsoni*. Fox (1989) re-examined Lillegraven's original materials and noted that on four M3s assigned to *A. wilsoni* (UALVP 2467, 3532, 3708, 4014), stylar cusp D is larger than cusp C, the morphology characteristic of *A. marshi* (Lillegraven, 1969).

These examples suggested that the relative sizes of stylar cusps C and D showed individual variation such that this character could not be consistently used to distinguish *A. marshi* and *A. wilsoni* from one another. Fox (1989) also noted that there were problems with Lillegraven's size criterion for separating *A. wilsoni* from *A. marshi*. Fox plotted the anterior-posterior lengths for M1/m1s, M2/m2s, and M3/m3s referred to these two taxa from the Lance (Clemens, 1966), Trochu (Lillegraven, 1969), Flat Creek (Hell Creek Formation, Montana, Archibald, 1977, 1982) and Wounded Knee (Frenchman Formation, Saskatchewan, Fox, 1989) local faunas. As Fox noted, *A. marshi* and *A. wilsoni* can be clearly separated on the basis of differences in molar size at **each** of the local faunas, but that this separation is not as distinct **between** localities. For example, anteroposterior lengths for M1s of *A. marshi* from the Lance and Flat Creek local faunas fall into the upper range of these lengths for *A. wilsoni* from the Trochu fauna (Fox, 1989· fig. 4). The same situation occurs for the M2s, though specimens from the Lance local fauna do also fall into the size range for *A. marshi* from the Trochu local fauna. The separation is more distinct for the M3s, where specimens referred to both species show generally consistent ranges between the local faunas, but Fox (1989) noted that M3s assigned to *A. marshi* from the Scollard Formation are anomalously large relative to M3s from the other localities. Fox (1989) questioned the validity of the biological units (i.e., species) represented by these specimens from the four local faunas, since there is considerable overlap between *A. marshi* and *A. wilsoni* in molar size measurements as well as in the relative sizes of stylar cusps C and D on M3. To illustrate this uncertainty, Fox referred specimens from the Wounded Knee locality to *Alphadon* sp. and *Alphadon*, cf. *A. wilsoni*, and suggested that the dental variation in *A. marshi* and *A. wilsoni* needed to be better understood.

Additionally, several researchers have noted that *Alphadon marshi* may be a composite taxon (Krishtalka and Stucky, 1983b; Russell, 1984; Cifelli, 1990a) in that some referred upper molars show a distinctly V-shaped centrocrista with the apex of the centrocrista directed towards the stylar shelf, including UALVP 2846, Scollard Formation, referred to *A. marshi* by Lillegraven (1969: fig.15.3a, **Plate 12**). This condition of the centrocrista is associated with "didelphid dilambdodonty" (Crochet, 1979, 1980, 1984; Reig et al., 1987), "a greater development of dilambdodonty" (Krishtalka and Stucky, 1983a: 256), "distinctly V-shaped centrocrista" (Cifelli, 1990a: 315), or simply "dilambdodonty" (Marshall and de Muizon, 1988; Marshall et al., 1990). Other upper molars referred to *A. marshi* also show a V-shaped centrocrista directed towards the stylar shelf (YPM 13659, the type specimen of *A. marshi*, **Plate 11A**), but would not be associated with "didelphid dilambdodonty", and clearly differ from molars described above

(**Plate 12A**). Krishtalka and Stucky (1983a: 254) use the term "incipient dilambdodonty" to describe this particular state, but the simple association of a "V-shaped centrocrista, directed towards the stylar shelf" with the state "dilambdodonty", whether "incipient", or showing a "greater development", cannot adequately separate these two morphologies. Both show a V-shaped centrocrista that is directed towards and reaches the level of the lingualmost part of the stylar cusp row. These morphologies themselves are distinct in many other features, including the depth and shape of the valley between the paracone and metacone, and can be easily distinguished from one another. The term "dilambdodont" will be applied to only one, as discussed below.

An examination of Lillegraven's materials from the Trochu local fauna, and materials from the Wounded Knee, Gryde, Lance, and Flat Creek faunas suggest that these **two** distinct and consistently distinguishable upper molar morphologies occur not only within *A. marshi*, as discussed above, but in *A.wilsoni* as well. Thus, both *A. marshi* and *A. wilsoni* are composite taxa and require revision. These upper molar morphologies concern not only the shape of the centrocrista, but also the shape, depth and orientation of the valley between the paracone and metacone (as circumscribed by the centrocrista), the shape of the labial faces of the paracone and metacone, the orientation of the postparacrista and premetacrista relative to the level of the stylar shelf (R. C. Fox, pers. comm., 1991), the postition of stylar cusp C relative to the apex of the centrocrista, and the depth of the trigon basin relative to the stylar shelf (Rigby and Wolberg, 1987; J. A. Case, pers comm., 1991). One of these morphologies corresponds most closely to that described in Clemens' (1966: 5) revised diagnosis of *A. marshi*, while the second is represented in specimens referred to a new species of *Alphadon* s.l., *A. jasoni* (Gryde locality, Saskatchewan, Storer, 1991). A new *A. marshi* sensu stricto is erected, differing from the former *A. marshi* s.s (Lillegraven, 1969), which was based primarily on molar size, relative sizes of stylar cusps and various premolar characters. The morphology associated with the new *A. marshi* s.s. follows the revised diagnosis of Clemens, so that some specimens previously referred to *A. marshi* s.l. can be assigned to this restricted concept of *A. marshi*, while others are instead assigned to *A. jasoni*. The morphology of the type specimen of *A. wilsoni* (UALVP 3681, **Plate 11B**) and certain specimens in the hypodigm of this species correspond to that described in Clemens' (1966) revised diagnosis for *A. marshi* s.s., so that *A. wilsoni* is a junior subjective synonym of *A. marshi* s.s. Other specimens of *A. wilsoni* can be referred to the new species, *A. jasoni*. As suggested above, these revisions are based on an examination of the morphology of the upper molars, and do not take into account the morphology of the lower molars, the M4s, or the premolars, as these do not show a consistently distinct morphology comparable to that for the upper molars. This is a problem, and one that is found in most studies of Late Cretaceous marsupials. Assignment of lower molars to various species is usually accomplished by finding size similarities between the upper molars and these dental elements (e.g., Clemens, 1966). A potential method for separating lower molars and referring them to *A. marshi* s.s. and *A. jasoni* based on the size of the hypoconid and the distance of the hypoconid from the protoconid will be discussed, but is not used in the revision below.

Alphadon marshi Simpson, 1927
Plates 11, 13

Alphadon wilsoni Lillegraven, 1969

Holotype: YPM 13659, right M3.

Horizon and type locality: Lance Formation, Niobrara County, Wyoming (Simpson, 1927).

Referred upper molars and distribution: **Lance Formation,** Wyoming (Clemens, 1966, not all of Clemens' materials were available for examination); UCMP 51428 (R max w/ M3, alveoli M4), 46885 (L max. w/M1-2), 47464 (LM1), 53155 (RM2), 52450 (RM3), 51428 (M3), 52502 (M2), 45601 (M2), 52715 (M2), 52767 (M3), 46805 (M3), 47544 (M1or M2), 52771 (M2), 53013 (M2), 48218 (M2), 52764 (M3), 46941 (M1); **Hell Creek Formation,** Montana (Archibald, 1977, 1982); UCMP 110542 (M3), 117678 (RM3), 11674 (RM2); **Scollard Formation**, Alberta (Lillegraven, 1969); UALVP 4020, 3023, 3080, 2720, 2615, 3942, 2815, all M1s; 2503, 3221, 2539, 3666, 2907, 2490, 3586, 2738, 2222, 2223, 4042, 2667, all M2s; 3797, 2567, 2921, 3156, 2467, 2414, 2387, M3s; **Frenchman Formation,** Saskatchewan (Fox, 1989); UALVP 22684 (RM2), 22724 (?M1), 22723 (?M2); **Naashoibito Member, Kirtland Formation,** New Mexico (Flynn, 1986); UALP 13633 (RM3), 13634 (LM2), 15712 (RM1 or 2), 15650 (LM2 or 3); **Fruitland Formation and/or "transition" and lower Kirtland Formation,** New Mexico (Rigby and Wolberg, 1987); UNM-B1743 (M2), UNM-B1740 (M3).

Revised diagnosis. See Clemens (1966: 5); in addition, stylar cusp C at deepest part of ectoflexus or slightly anterior; labial faces of paracone and metacone conical, not flattened and concave; centrocrista V-shaped, apex sharp, positioned at lingual face of stylar cusp C; valley between paracone and metacone long, wide, shallow; postparacrista and premetacrista run ventrally from apices of paracone and metacone to level of stylar shelf with little horizontal component; level of trigon basin floor closer to that of stylar shelf; upper molars not dilambdodont.

Description. The following description will be for M1-3, and differences between these molars will be discussed afterwards. Stylar cusp A is large and ventrally or basally positioned relative to stylar cusp B. Cusp B is the largest cusp on the stylar shelf, positioned labial to the paracone and connected to this cusp by the preparacrista. A crest runs anteriorly from stylar cusp B to cusp A, and posteriorly, to the labial edge of the stylar shelf. Stylar cusp C is consistently present and oriented anteroposteriorly, is conical, smaller than B, and is lingually positioned away from the edge of the stylar shelf, at or only slightly anterior to the deepest part of the ectoflexus. Stylar cusp D is smaller than B but larger than cusp C and extends along the posterior edge of the shelf. The stylar shelf is narrower anteriorly on M1, increases in width on M2 and is more equal in width to the posterior stylar shelf on M3, such that the paracone and cusp B are more closely appressed on M1 and M2, but further separated on M3. The length of the preparacrista lengthens concomitantly. The ectoflexus deepens from M1 to M3. These latter two trends are seen in most species referred to *Alphadon* s.l. The paracone and metacone are subequal in height, with the metacone being wider than the paracone in labial view. These cusps are more widely separated on the occlusal surface. The crests making up the centrocrista (postparacrista and premetacrista) run ventrally from the apices of the paracone and metacone to the apex of the centrocrista, with little horizontal component at the level of the stylar shelf. The apex of the centrocrista is positioned at the lingual base of stylar cusp C. The valley between the paracone and the metacone (delineated by the postparacrista and premetacrista) will be described in terms of molar dimensions given by Clemens (1966) and Lillegraven (1969), that is, in terms of anteroposterior length and transverse width. As well, the depth of the valley will be described in terms of the height of the walls of this valley, or in other words, the height of the crests of the centrocrista above the trigon basin. These comparisons are qualitative (i.e., anteroposteriorly shorter or longer) and are diagrammed in **Figure 14** (as briefly mentioned in the discussion of *Protalphadon* n. sp. A). In *A. marshi* s.s., the valley between the paracone and metacone is anteroposterior longer, and transversely wide, reaching the level of the lingual base of the stylar cusp row. However, this valley is shallow, as the walls decrease in height from the apices of the paracone and metacone to the apex of the centrocrista. This is correlated with the character state given in the diagnosis, "postparacrista and premetacrista run ventrally from the apices of the paracone and metacone, with little horizontal component". The conules are strong and equally distant from the paracone and metacone. The internal conular cristae are also strong and well developed. The anterior and posterior cingula are well developed. The protocone is longer anteroposteriorly, but is not expanded basally, and there are no protoconal cingula present. See Clemens (1966: 5-8, 87-90) and Lillegraven (1969: 33-49), for descriptions of lower molars, premolars and M4. These specimens are not included in the hypodigm because of the difficulty in consistently separating materials once placed in *A. marshi* s.l. and *A. wilsoni* and assigning them to *A. marshi* s.s. and *A. jasoni*.

Discussion. *Alphadon marshi* s.s includes materials once assigned to *A. marshi* s.l., as well as to *A. wilsoni*. The holotype of *A. wilsoni* (UALVP 3681) is a fragmentary right maxilla with M2-3. Though the teeth are worn, the similarity to *A. marshi* s.s. in the morphology of the valley between the paracone and metacone and the shape and orientation of the crests of the centrocrista are clear, especially when compared to molars of *A. wilsoni* assigned below to *A. jasoni* (**Plate 12, 14**). A further discussion is given in conjunction with that given for *Alphadon jasoni*.

Alphadon jasoni Storer, 1991
Plates 11, 14, 15

Holotype. P2004.4, RM^2

Horizon and type locality. Gryde locality, Frenchman Formation (Maastrichtian), southwestern Saskatchewan (Storer, 1991)

Referred upper molars and known distribution. **Lance Formation**, Wyoming; UCMP 51427 (maxillary fragment preserving M1-2), 53097 (M3); **Frenchman Formation** (Gryde and Wounded Knee localities), see Fox, 1989 and Storer, 1991, all specimens referable to *A. jasoni*; except for those listed in the hypodigm for *A. marshi* s.s.; **Scollard Formation**; UALVP 3945, 4023, 3490, 2822, 2316, 2221, 2473, 3806, 2728, M1s; 3956, 3346, 2656, 2313, 2309, 2219, 652, 3668, 3151, 3740, 3241, 2814 M2s; 3807, 3708, 3478, 3236, 2224, M3s; **Ravenscrag Formation** UALVP 18351, 18352, M2s, Johnston and Fox, 1984; **Hell Creek Formation**; UCMP 117698, 117699, 117700, 117701, 117702, M1s; 117703, 117704, 117705, 117706, 117707, M2s; 109030, 117708, 117709, M3.

Revised diagnosis. See Storer, 1991: 356, additionally, stylar cusp C anterior to the deepest part of the ectoflexus on M1-3; paracone and metacone labial faces flattened to concave, apices appear shifted lingually relative to edge of stylar shelf; centrocrista V-shaped, centrocrista apex rounded, positioned posterior to lingual base of stylar cusp C; valley between paracone and metacone narrower and deeper (than in *A. marshi* s.s.), walls of preparacrista and postmetacrista high (relative to level of trigon basin) from apices of paracone and metacone to apex of centrocrista; preparacrista and postmetacrista run for part of their length horizontally at level of stylar shelf; depth of trigon basin greater, relative to level of stylar shelf; upper molars dilambdodont.

Description. See Storer, 1991: 356-357, for a complete description; additionally, the valley between the paracone and metacone is narrower, but is as wide as in *A. marshi* s.s., since in both taxa, this valley (as delineated by the apex of the centrocrista) reaches the lingual edge of the stylar cusp row. In *A. jasoni*, the valley is deeper, as the walls of the preparacrista and the postmetacrista are high, from the apices of the paracone and the metacone to the apex of the centrocrista. This is correlated with the horizontal orientation of the preparacrista and the postmetacrista at the level of the stylar shelf, for at least some part of the lengths of these crests. The apex of the centrocrista reaches the stylar cusp row at a point posterior to stylar cusp C. Storer's specimens from the Gryde locality are morphologically similar to the specimens referred to *A. jasoni* from the various localities above, but there are some small differences in stylar shelf morphology between M3s of *A. jasoni* from the Gryde locality, and M3s from the Wounded Knee locality (Fox, 1989). On the M3s from the Gryde locality, the bases of stylar cusp B and the paracone almost meet. This is the same condition seen in several specimens from the Lance fauna (for example, UCMP 51385, Clemens, 1966), while in M3s from the Wounded Knee fauna, cusp B and the paracone are more widely separated on the anterior stylar shelf. This is also seen on M3s from the Trochu local fauna (UALVP 2846, Lillegraven 1969), as well. The significance of this difference has not yet been determined, but may have to do with the sizes of the paracone and cusp B relative to the width of the stylar shelf, which would affect the length of the preparacrista, and the length of the shearing surface associated with this crest. In the case of *A. jasoni*, the more closely approximated paracone and stylar cusp B would result in a shorter preparacrista, and a reduced emphasis on shear. A reduced emphasis on shearing is often associated with an increased emphasis on crushing, which does not appear to be the case for upper molars referred to *A. jasoni* as a whole. For the moment, the relative differences in the separation of cusp B and the paracone on certain M3s of *A. jasoni* will be considered to be due to individual variation. Differences in the separation of cusp B and the paracone for M1s and M2s are more difficult to evaluate, as these cusps are more closely approximated on these teeth as one of the morphological trends from M1-3 in species of *Alphadon* s.l. As well, Storer (1991) noted differences in the relative sizes of stylar cusps B and D for *A. jasoni* and upper molars previously referred to *A. marshi* s.l. and "*A. wilsoni*". Again, these differences are accounted for here by individual variation within *A. jasoni*.

Discussion. Storer (1991: 358) noted that *A. jasoni* was represented by a large number of specimens from the Gryde local fauna, in the absence of the normally widely distributed *A. wilsoni* and *A. marshi*. The revisions presented above suggest instead that two separate upper molar morphologies are present in the *A. marshi- A. wilsoni* complex, and that one of these morphologies corresponds to that described for *A. jasoni*. Therefore, *A. jasoni* does not occur in the absence of *A. marshi* and *A.wilsoni*, as suggested by Storer (1991), but rather, elements of *A. jasoni* had previously been referred to these two taxa. Some figured specimens of *A. marshi* s.l. (i.e., Lillegraven, 1969: fig. 15.3a) had caused confusion because the morphology of these (particularly in the shape of the centrocrista) was more similar to specimens assigned to the the Family Didelphidae (Cifelli, 1990a). Other specimens of *A. marshi* s.l. from various faunas possess a similar morphology (Cifelli, 1990a), as do several specimens assigned to "*A. wilsoni*". However, these Late Cretaceous materials are referred to *Alphadon jasoni*, rather than any taxon within the Family Didelphidae, for reasons discussed below. This upper molar morphology of *A. jasoni* corresponds to the condition called "dilambdodonty" or "didelphid dilambdodonty" by various authors. This morphology is considered to be a synapomorphy for the Family Didelphidae or the Tribe Didelphini (Crochet, 1979, 1980; Krishtalka and Stucky, 1983b; Marshall and de Muizon, 1988; Marshall et al., 1990). However, "dilambdodonty", as applied to marsupial taxa, seems to have come to refer simply to a V-shaped centrocrista with the apex directed towards the stylar shelf or stylar cusp C (Crochet, 1979, 1980, 1984, 1986; Reig et al., 1987; Marshall and deMuizon, 1988; Van Valen, 1988; Cifelli, 1990a; Marshall et al., 1990). The term dilambdodont as originally used by Gill (1884: 136) actually refers to the two crests of the centrocrista as well as the preparacrista and the postmetacrista (in combination called the ectoloph), with these being strongly developed (also Robinson, 1968; Hershkovitz, 1971; Setoguchi, 1975, 1978; Crochet, 1980, Butler, 1982; Russell, 1984; Cifelli, 1990a). However, since the state of the centrocrista on the dilambdodont molar is more easily recognizable than that of the preparacrista and the postmetacrista (i.e., in terms of strength of development), the attention of various researchers has focused on the morphology of the centrocrista to distinguish between dilambdodonty, and the condition in which the upper molars show a straighter centrocrista, called predilambdodonty (or prédilambdodontie of Crochet, 1980; also rectidodont, Van Valen, 1988).

Actually, Gill (1884: 136) first applied the term dilambdodont to the Insectivora, saying that some insectivorans had “oblong molars with two V-shaped (W) ridges...[t]hose with two V-shaped ridges are called Dilambdodonta”. Therefore “dilambdodont” originally had descriptive and taxonomic applications. Simpson (1931) suggested that the Dilambdodonta was not a natural phylogenetic unit and that this taxonomic name should be abandoned, with the term dilambdodont being used for descriptive purposes alone. It is important to note that the original definition, as provided by Gill (1884), only describes two V-shaped ridges on the upper molars, and makes no reference to the depth or labial extent of the valley between the metacone and the paracone. Butler (1939, 1941) divided mammalian molars into four types, including tritubercular, zalambdodont, dilambdodont and quadritubercular. Butler differentiated between these types primarily on the basis of the sizes of the paracone and metacone, the positions of these cusps relative to the buccal edge of the molar, and the development of the buccal area (stylar shelf). On dilambdodont molars, the paracone and metacone were said to be subequal, further removed from the buccal edge of the molar, with the buccal area of the molar being well developed. Tritubercular molars had a more buccally placed paracone and metacone, and a poorly developed stylar shelf. Taxa possessing dilambdodont molars included *Tupaia*, the eutherian orders Soricoidea (insectivorans), Chiroptera (bats), Dermoptera (flying lemurs), and in the Marsupialia, the families Dasyuridae, Peramelidae and Didelphidae, including what were classified as Upper Cretaceous didelphids at that time (Butler, 1941: 434). This definition of dilambdodont upper molars differs from that given by Gill (1884), and used by most researchers today in its lack of focus on the crests joining the paracone and metacone. Butler (1939: 13) did note that on upper molars of *Didelphis*, the paracone and metacone are separated by a V-shaped "cleft" that did not extend as far buccally as did the "cleft" in *Tupaia*, and discussed the separation of the paracone and metacone by a deep, V-shaped groove (Butler, 1941: 428, 437) in Soricoidea, *Tupaia*, and many bats, but not in *Didelphis*.

Crochet (1979, 1980: 28-9) provided a revised definition of the dilambdodont morphology in order to accommodate the morphology seen in some Tertiary marsupial taxa (i.e., *Peratherium*). As discussed in Chapter 1, Crochet differentiated between "dilambdodontie didelphienne" (didelphid dilambdodonty), as seen on upper molars of *Peratherium*, and "dilambdodontie talpedienne" (talpid dilambdodonty). For the former, Crochet (1980: 29) notes, "la centrocrista n'attient pas le bord labial de la couronne ni les cuspides stylaires qui peuvent s'y trouver.", and for the latter (ibid.: 29), "la centrocrista rejoint le mésostyle qui peut être unique... ou dédoublé". Crochet (1980: 29) also provides a definition for "prédilambdodontie" in which the centrocrista is straight, or shows some tendency towards dilambdodonty. In didelphid dilambdodonty, Crochet clearly states that the apex of the centrocrista does not reach the level of the stylar shelf, and provides a figure

(Crochet, 1980: fig. 4b) of an M3 of *Peratherium cuvieri* (Fischer, 1829) as an example. In a later paper however, Crochet (1984) suggests that in didephid dilambdodonty, the centrocrista meets the lingual base of stylar cusp C, when he notes (ibid.: 280) in his description of the new species *Garatherium mahboubii* Crochet, 1984 that, " La centrocrista est en forme V dont les deux branches après s'être rejointes se poursuivent par une crête qui atteint la base lingual de la cuspide C.", and for upper molars referred to this species "... ce dernier type [didelphid dilambdodonty] de dilambdodontie est accuse: la centrocrista rejoint la base linguale de la cuspide stylaire C.". On upper molars referred to *A. marshi* s.s. and *A. jasoni* the apex of the centrocrista reaches the lingual base of stylar cusp C, and therefore, the term "didelphid dilambdodonty" could be applied to *A. jasoni* **and** to *A. marshi* s.s., even though upper molars referred to *A. marshi* s.s. are not called dilambdodont in the diagnosis given above.

There is potential for confusion in continuing to apply the term "dilambdodonty" or "didelphid dilambdodonty" to upper molars with two V-shaped ridges, or with a W-shaped ectoloph, such that the centrocrista is V-shaped, with the apex of this V directed towards the stylar shelf and meeting the lingual base of stylar cusp C. On upper molars referred here to *Alphadon marshi* s.s, including the type specimen (**Plates 16B, 17B**), the centrocrista is clearly V-shaped, with the V directed towards the stylar shelf and reaching the lingual base of stylar cusp C. This is implied in the diagnosis of *A. marshi* given by Clemens (1966), even though he refers to the valley between the paracone and metacone as reaching the lingual base of stylar cusp C, rather than the apex of the centrocrista. Therefore, upper molars of *A. marshi* s.s could be described as possessing a didelphid dilambdodonty, and could be coded as such in a phylogenetic analysis. On upper molars referred to *A. jasoni* (**Plates 16A, 17A**), the centrocrista is again V-shaped, with the apex directed towards the stylar shelf and reaching the base of stylar cusp C, though just posterior to this cusp, rather than directly at its lingual base. These molars could therefore also be called dilambdodont. Even a cursory examination of the molars referred to these two taxa (compare **Plates 16A, B and 17A, B**) suggests that a use of the term "dilambdodonty" would not be equivalent for both. By applying this term as it has been in recent studies, one is unable to differentiate between the condition in *A. marshi* s.s. and in *A. jasoni*. Krishtalka and Stucky (1983a: 254) used the term "incipient dilambdodonty" to describe upper molars referred here to *A. marshi* s.s, but this term refers to a condition where "the centrocrista or just the premetacrista is directed towards the stylar shelf". The reference to the premetacrista alone is confusing, and in any event, "incipient dilambdodonty" still refers to some V-shaped condition of the centrocrista. As suggested in the revised diagnosis of *A. marshi* s.s. given above, the term dilambdodonty should not be applied to this taxon, and requires a more precise definition.

"Dilambdodonty" is considered to be characteristic of the Family Didelphidae (Crochet, 1980; Marshall and de Muizon, 1988), and upon examining upper molars of some of the referred taxa, it is clear what type of molar morphology has been associated with dilambdodonty by various researchers (i.e., Crochet, 1980; Fox, 1983: fig. 2; Krishtalka and Stucky, 1983b: fig. 2A, for some of the better figures provided). In these forms, the centrocrista is V-shaped, with the apex being directed towards the stylar shelf, but in addition, the crests making up the centrocrista have some labiohorizontal component along the stylar shelf (R. C. Fox, pers. comm., 1991), so that the walls of the postparacrista and the premetacrista (from the crest itself to the floor of the trigon basin) are very high (Butler, 1982), and the valley between the paracone and metacone is very deep. This is an important point of difference with the morphology seen in *A. marshi* s.s., where the postparacrista and premetacrista extend ventrally or basally from the apices of the paracone and metacone, such that the walls of the postparacrista and the premetacrista are lower and the valley between these cusps is shallower. Therefore, the term "dilambdodonty", as used here, will not only refer to the shape of the centrocrista, or to the morphology of this crest and the preparacrista and postparacrista (=the ectoloph), but also to the morphology of the valley between the paracone and metacone (Butler, 1982).

The first upper molar morphological category recognizable in the *Alphadon marshi-A. wilsoni* complex, and observed on upper molars referred to *A. jasoni*, shows the dilambdodont condition. On these upper molars, the valley between the paracone and metacone is narrower and deeper, and the walls of the postparacrista and the premetacrista are high. These crests run ventrally from the apices of the paracone and metacone to the stylar shelf, but then have a labiohorizontal component at the level of the stylar shelf. Some features seem to be associated with this dilambdodonty, for example, the apex of the centrocrista is rounded, and reaches the lingual base of the stylar cusp row posterior to stylar cusp C. Cusp C is positioned anterior to the deepest part of the ectoflexus. The trigon basin is more basally placed on the tooth, relative to the level of the stylar shelf (contrary to the suggestion of Rigby and Wolberg (1987: 63), that the trigon basin is much deeper than the stylar shelf in *A. marshi*; these authors are instead describing the state seen in *A. jasoni*). The shape of the labial faces of the paracone and metacone are flattened to concave rather than conical. Storer (1991) noted that specimens from the Wounded Knee locality referred by Fox (1989) to *Alphadon* sp. could be assigned to *A. jasoni*. As well, several specimens assigned to *A. wilsoni* and *A. marshi s.l.* can be referred to *A. jasoni*, as listed above.

The second upper molar morphological category corresponds most closely to that given in the revised diagnosis of *A. marshi* s.l. by Clemens (1966). Part of Clemens' revised diagnosis (1966: 5) includes the following: "...stylar cusp C large and well separated from B, C usually in a central position on the stylar shelf but on a few teeth it is on the labial margin ... paracone and metacone separated by a broad valley that, on most teeth, ends at the lingual side of stylar cusp C." A re-examination of materials referred to *A. marshi* s.l. by Clemens (1966, and UCMP materials) indicates that the majority show an upper molar morphology in which stylar cusp C is positioned at the deepest part of the ectoflexus, the apex of the centrocrista meets the stylar shelf lingual to stylar cusp C rather than posterior to this cusp, and the apex of the centrocrista is V-shaped. The postparacrista and the premetacrista run ventrally from the paracone and metacone to the stylar shelf, with little or no labiohorizontal component, so that the walls of the postparacrista and the premetacrista are lower and the valley between the paracone and metacone is shallower. The valley between the paracone and the metacone is also anteroposteriorly longer, and the trigon basin is not as basal relative to the level of the stylar shelf. These character states are part of, or can be associated with, the upper molar morphology that is described in the revised diagnosis of *A. marshi* s.l. (Clemens, 1966). Simpson (1929: fig. 45f) figured the holotype (YPM 13659, RM3) of *A. marshi* s.l., but did not list or discuss additional specimens. This specimen is figured in **Plates 11B, 16B and 17B**, and possesses the upper molar morphology discussed in Clemens' revised diagnosis of *A.marshi*. Though type specimens need not be typical of the taxon they represent (i.e., Raup and Stanley, 1971: 106), they do provide guidelines for taxonomic changes (Langston et al., 1977; Wiley, 1981). This was well illustrated in the revision of *A. creber* presented earlier. Since the holotype of *A. marshi* possesses the morphology described in Clemens' (1966) revised diagnosis of this taxon, *A. marshi* should be restricted to upper molar specimens that possess this morphology. Clemens' diagnosis provides the basis for the latest revised diagnosis of *A. marshi* given above. This diagnosis does not alter the one given by Clemens, only adding information regarding the morphology of the valley between the paracone and the position of stylar cusp C relative to this valley. Upper molars once referred to *A. wilsoni*, including the holotype (UALVP 3681, **Plate 11B**) and certain specimens from the original hypodigm (**Plate 13**), are referred to this restricted *A. marshi*, such that *A. wilsoni* is a junior subjective synonym of *A. marshi* s.s. Other upper molar specimens referred to *A. wilsoni* from various localities may instead be referred to *A. marshi s.s.*, and these are listed in the "Systematic Paleontology" section.

Though molar size (anterior-posterior length and transverse width and ratios of these) has formed part of the basis for separating "*Alphadon wilsoni*" from *A. marshi*, it is apparent from the discussion above that the morphology of the occlusal surface is more important in the revision of these species (contra Lillegraven, 1969; Clemens, 1973; Fox, 1989). Lillegraven (1969; also Clemens, 1973) noted that molars referred to "*A. wilsoni*" were significantly smaller, but proportionately longer (i.e., having a higher anteroposterior length/ transverse width ratio), than those referred to *A. marshi* s.l., but Fox (1989) demonstrated that these size differences, at least in terms of anteroposterior length, were not consistent from locality to locality. The use of morphological features in separating taxa (i.e. dilambdodonty vs. non-dilambdodonty) is generally preferable to the use of molar size since the number of molars available for study are relatively small, and many of these are damaged, making it difficult to accumulate a large number of measurements in order to determine what size differences are significant at the species level. For example, several upper molars once referred to those of "*A. wilsoni*" have been assigned above to *A. marshi* s.s. and to *A. jasoni*. Storer (1991) noted that specimens assigned to *A. jasoni* from the Gryde locality were similar to "*A. wilsoni*" in size, while Fox (1989; also Cifelli, 1990) stated that materials from the Scollard Formation (Lillegraven, 1969) assigned to *A. marshi* (but here referred to *A. jasoni*) were unusually large. As well, Clemens (1966) observed a bimodality in size measurements for molar specimens from the Lance formation he referred to *A. marshi*. Later, Clemens (1973) followed the suggestion of Lillegraven (1969), and separated the smaller of these specimens and assigned them to "*A. wilsoni*". An examination of a figure of one of these smaller specimens (Clemens, 1966: fig. 2) shows that the morphology of the upper molars preserved on this specimen corresponds to the revised diagnosis of *A. marshi* (Clemens, 1966), and as discussed above, this specimen, and other like it, must be retained in *A. marshi* s.s.

Statements like these suggest that there is a wide range of molar sizes of specimens referred to *A. jasoni*, and to a lesser extent, for *A. marshi* s.s. Do specimens of "*A. wilsoni*" now represent the lower range of size values for *A. marshi* s.s. and *A. jasoni*, or should the larger specimens (particularly those from the Scollard Formation) referred to *A. jasoni* and the smaller specimens referred to *A. marshi* be assigned to a new species? The morphologies associated with *A. jasoni* and *A. marshi* s.s. are distinct, and consistently distinguish these two species; however, when comparing specimens of *A. jasoni* (**Plate**

18A, C) formerly referred to "*A. wilsoni*", and similarly sized specimens from the Wounded Knee locality, Frenchman Formation (**Plate 18B**) with larger specimens from the Scollard Formation (**Plate 18D**), the size difference between these seems significant. Three scattergrams were produced for M1s, M2 and M3s (measurements recorded in **Table 2**) referred in this study to *A. jasoni* (**Figure 15A-C**). The dimension used in these figures was anteroposterior length of the molar, because this measurement was the one available for the largest number of specimens (since many were damaged), and Storer (1991) only included a value called "buccolingual diameter" in his measurements of *A. jasoni*, without clearly stating whether this was anterior or posterior width. The bulk of these measurements are for specimens from the Scollard and Frenchman formations, with fewer for specimens from the Lance formation. These latter specimens are stored in the UCMP collections, and though available for study, were not measured (nor were those from the Hell Creek formation, Montana (Archibald, 1977, 1982)).

These scattergrams indicate that for M1s and M2s, there are gaps in values for anteroposterior molar length between specimens from the Scollard Formation and all others. The separation is less distinct for M3s, but this may be due to the small number of measurements available for M3s from the Scollard Formation. The scattergrams suggest that there may be significant size differences between these specimens, and this is tested further through the use of a Student's t-test, which tests the degree of significance of these differences, and is appropriate for groups of specimens less than 30. The results of these t-tests are presented in Appendix 1, and show that the size differences (anteroposterior length) between the specimens from the Scollard Formation and specimens from others are significant, for M1-3. This suggests that the Scollard Formation specimens be referred to a new species, differing from *A. jasoni* only in size.

However, one problem in erecting taxa based on differences in molar size alone is that there does not seem to be enough information on what constitutes appropriate **molar size ranges** for fossil taxa like *A. jasoni*. Perhaps the wider variation in molar sizes within *A. jasoni* can be accounted for in these ranges. Molar size ranges are thought to be correlated with overall body size (Gingerich, 1974, 1976, 1977; Gingerich et al., 1982). Gingerich (1974) has suggested that molars are least susceptible to individual variation and variation due to sexual dimorphism, but Hough (1961: 219) noted that in didelphids, teeth show differences in size between the sexes and between individuals. If molar size is considered to be correlated with the overall size of the animal, then variations in body size should be reflected to some degree in variation in the size of the dentition. The use of molar size as an estimator of body mass has been criticized by various authors (Hylander, 1985; Damuth and MacFadden, 1990; Damuth, 1990; Janis, 1990; Jungers, 1990) on the basis that teeth do not have a biomechanical relationship to body mass (i.e., functioning in support) as would the various limb elements, so that there would less of a correlation between body mass and parts of the dentition. This suggestion is valid, but as teeth are the only elements available for *Alphadon* s.l. upon which to estimate body mass, they must be used.

These molar size ranges (and thus ranges in overall body size) would include or account for individual variation, differences due to sexual dimorphism, and variation between different geographical populations. Therefore, at least some approximation of these size ranges should be established for *A. jasoni* (and *A. marshi* s.s.), for example, by a comparison to molar size ranges from an extant marsupial species. To this end, ranges of upper molar sizes (lengths and widths) of geographically separate populations of the modern North American opossum *Didelphis virginiana* are tallied (**Table 3**); these molar sizes are again considered to be indicative of the actual size, in terms of body mass, of the animal. *Didelphis virginiana* was selected for this study because large numbers of male and female specimens are readily available from various localities across the United States. Skulls and mandibles of both male and female opossums were obtained from several institutions, and the lengths and widths of M1-3 measured (since lower and upper molars are strongly functionally related in the occlusal relationship, size trends in lower molars would follow those for the upper molars; therefore, lower molar measurements were not considered). Measurements were not taken from broken teeth, but were taken from worn teeth if it was felt that the size of the tooth was preserved. The majority of the specimens were marked as being either male or female; measurements taken from these individuals were separated and the means of these calculated. Certain individuals were not marked as being male or female, but so as not to waste any data, if the values of the measurements for these unknown specimens were above the mean for the measurements taken from the male specimens, they were added to the list of values for the males. If measurement from the unknown individual was lower, it was referred to the female list.

Though *Alphadon* s.l. and *Didelphis* were previously classified together in the Family Didelphidae (e.g., Simpson, 1929; Clemens, 1966), more recent classifications have removed *Alphadon* s.l. from this family (Crochet, 1979, 1980; Reig et al., 1985, 1987; Aplin and Archer, 1987; Marshall, 1987; Cifelli, 1900a; Marshall et al., 1990), suggesting that the two taxa are not as closely related as previously thought. Some researchers have suggested that when estimating body mass from skeletal elements (e.g., teeth) in extinct taxa from a correlation between these elements and body mass in extant taxa, it is more important these taxa show similarities in the functional relationships of these elements rather than any taxonomic relationship (Fortelius, 1990; Damuth, 1990; Janis, 1990). The overall functional similarity between *Alphadon* s.l. and *Didelphis* has been discussed by Crompton and Hiiemae (1969, 1970) and Hiiemae and Crompton (1971), but may be questioned because of the differences in molar morphology between the two taxa.

Regardless of the problems and uncertainties discussed above, the main concern of this exercise was to show that a geographically widespread taxon like *Didelphis virginiana* would show a wide range of variation in body size, as reflected in variation in the sizes of the upper molars. This variation is seen in **Figure 16A-C** and **Figures 17-19. Figure 16A-C** shows the ranges of measurements (anterior-posterior molar length) of M1s, M2s and M3s for both female and male specimens. **Figures 17-19** are histograms depicting the distribution of these upper molar measurements, again for female and male specimens. The specimens represented in these figures were collected from a wide variety of separate localities (Michigan, North Carolina, Indiana, Oklahoma, Nebraska, and Kansas). These figures suggest that there is a wide range of overall variation in molar sizes among individuals that are known to belong to a single species (*Didelphis virginiana*), and perhaps a wider range of variation could be expected for taxa like *A. marshi* s.s. and *A. jasoni*, which are known from geographically widespread localities, including Alberta, Wyoming, Montana, Saskatchewan and New Mexico. These figures also indicate that generally, anteroposterior lengths of molars of female specimens are smaller than those of male specimens, but that there is some degree of overlap, especially with regards to the female specimens. It may be premature to suggest that larger Scollard specimens referred to *A. jasoni* may represent males of the species; nevertheless, the figures for *D. virginiana* do indicate that there is some degree of separation in molar size between males and females within this species.

The hypothesis that molar size ranges recovered from populations of *D. virginiana* may provide a reasonable approximation of acceptable molar size (and thus overall body size) ranges for *A. jasoni* is tested further by means of a F-ratio (F distribution) of sample (representing population) variances. This test can indicate whether two population variances are equal, so that if the variance within the population represented by the sample of *A. jasoni* (including the larger Scollard specimens) is equal to that within the population represented by the sample of *Didelphis virginiana*, then this would be evidence that all specimens assigned to *A. jasoni* be retained within *A. jasoni*. The results are given in **Appendix 2**, and test the null hypothesis that the two population variances are equal. The alternative hypothesis is that the population variance in *Didelphis virginiana* is less than that in *A. jasoni*, and therefore that the variation in *A. jasoni* is greater than would be expected in a single species. The results of the F-ratio test show that for M1 and M2, the null hypothesis cannot be rejected, but that this hypothesis can be rejected for the M3s. Therefore, at least for the M1s and M2s, the population variance within *A. jasoni* does not exceed that within the extant species, *Didelphis virginiana*.

The results of the statistical tests employed above suggest that the Scollard specimens assigned to *A. jasoni* represent a new species (from the t-test), but also that these specimens do not represent a new species (from a comparison of the ranges of *A. jasoni* and *Didelphis virginiana* visually and for the most part through the F-ratio test). These differing results, the validity of using *Didelphis virginiana* as an appropriate comparison to *A. jasoni*, and the very apparent differences in molar size between the Scollard specimens and others referred to *A. jasoni* (**Plate 18**) suggest that the best route to take is to tentatively separate the Scollard specimens from *A. jasoni*, but to retain this new species in open nomenclature until more data are found. The larger Scollard specimens are referred to *Alphadon* sp., cf. *A. jasoni* (including UALVP 2846, M1-4, p3-M4; 2901, 2982, 4071, 2437, 2994, M1s; 2758, 2621, 2819, 2452, M2s; 2472, 2427, M3s; some of these shown on **Plate 19**), which emphasizes their distinctiveness from *A. jasoni*, but still suggests that more information is needed. Erecting a new species for these specimens would require data (in the form of molar measurements) from more of the Lance and Hell Creek specimens referable to *A. jasoni* (Clemens, 1966; Archibald, 1977, 1982), as well as a larger number of specimens (especially M3s), from the Scollard and other contemporaneous formations. Because *Alphadon* sp. cf. *A. jasoni* differs from *A. jasoni* in size alone, it is not included in the phylogenetic analysis, but will be added to the final classification.

This revision of *A. marshi* and "*A. wilsoni*" has resulted in "*A. wilsoni*" being placed in synonomy with *A. marshi* s.s. and certain specimens from both "*A. wilsoni*" and *A. marshi* s.l. being placed in the new species, *A. jasoni*, on the basis of the morphology of the centrocrista, the depth and orientation of the valley between the paracone and metacone, the height of the stylar shelf above the trigon basin and other associated characters, as described above. Upper molars referred to *A. jasoni* were described as being dilambdodont, while dilambdodonty has been described as a synapomorphy for the Family

Didelphidae (Marshall and de Muizon, 1988). Russell (1975: 155, 1984) suggested that *Alphadon* s.l. was ancestral to *Peratherium* (Family Didelphidae), presumably because of the dilambdodont morphology seen in *Peratherium* and on some specimens assigned to *A. marshi* s.l.(i.e. UALVP 2846). Cifelli (1990a: 316), referring to *A. marshi* s.l., noted that this species may be referable to the Family Didelphidae, on the basis of the possession of dilambdodont upper molars. These upper molars were removed from *A. marshi* s.l. and assigned to *A. jasoni*, but it is still possible that *A. jasoni* should be classified in the Family Didelphidae, posssessing a closer relationship with members of the Subfamily Herpetotheriinae, including taxa such as *Peratherium* and *Herpetotherium*. The other possibility is that the dilambdodont condition is convergent or independently acquired in members of the Family Didelphidae and *A. jasoni*. Though noting that specimens referred to *A. marshi* s.l. might be assigned to the Family Didelphidae, Cifelli (1990a: 315-16) strongly suggested that this dilambdodonty was homoplasious in *A. marshi* s.l. (specimens here referred to *A. jasoni*) and other marsupial taxa, since this morphology occured independently at least twice in taxa from the late Paleocene Itaborai fauna of Brazil (also Marshall, 1987 for the Itaborai fauna, and Marshall in Marshall et al., 1990: 461-62, for South American taxa in general).

The classification of *Alphadon jasoni* in the Family Didelphidae is not supported here, and the dilambdodont morphology is believed to have been acquired independently in the two taxa, because although there are similarites, there are also important differences between the morphology of upper molars referred to *A. jasoni* and to members of the Subfamily Herpetotheriinae, Family Didelphidae. For example, the paracone and metacone of *A. jasoni* are subequal (**Figure 20**, contrary to the suggestion of Cifelli, 1990a, that some specimens here referred to *A. jasoni* show a shorter paracone relative to the metacone), while the paracone is greatly reduced relative to the metacone in members of the Herpetotheriinae, said to be another synapomorphy for the Family Didelphidae as a whole (Crochet, 1979, 1980; Krishtalka and Stucky, 1983b; Reig et al., 1987; Marshall, 1987; Marshall and de Muizon, 1988; Marshall et al., 1990), but also shared by *Peradectes*, as discussed in Chapter 2. Admittedly, wear on the paracone and metacone frequently makes it difficult to assess the relative heights of these cusps, but on several well preserved specimens assigned to *A. jasoni* (P2004.4 (holotype), P1927.594; P1927.660; UALVP 2846, 2210, 2452, 3708), the paracone and metacone are clearly subequal in height (**Figure 20**). The paracone is narrower than the metacone on these specimens, this being especially evident in labial view. The differences in the relative heights of the paracone and metacone have important functional implications that suggest that specimens assigned to *A. jasoni* should not be assigned to the Subfamily Herpetotheriinae.

To examine these differences and their implications, the upper and lower molars of the herpetotheriines and *Alphadon jasoni* should be viewed as functional units, so that morphological features on the uppers are correlated with features on the lowers and vice versa, as discussed in Chapter 2. The relationship between the crests of the centrocrista (upper molars) and of the hypoconid (lower molars) as the hypoconid moves past the centrocrista during the chewing cycle, to occlusion, were also discussed in Chapter 2. This discussion suggested that a labial shift in the location where the cristid obliqua meets the posterior wall of the trigonid would result in a reduction in the length of the cristid obliqua. This reduction in the length of the cristid obliqua would be correlated with a reduction in the length of the postparacrista and a reduction in the size or height of the paracone, relative to the metacone. This morphological relationship is seen on upper and lower molars referred to *Peratherium*, but on molars referred to *A. jasoni*, the paracone and metacone are subequal in height, and the cristid obliqua is more lingually placed (basal to the postcristid notch), and is longer, than on lower molars referred to *Peratherium*. On lower molars referred to *Peratherium*, the cristid obliqua meets the posterior wall of the trigonid at a point labial to the postcristid notch. This is one point of difference between *A. jasoni* and members of the Subfamily Herpetotheriinae, even though upper molars referred to both possess a dilambdodont morphology.

Another difference between *Alphadon jasoni* and the herpetotheriines involves the position of the hypoconulid relative to the entoconid on the lower molars. In the herpetotheriines (e.g., *Herpetotherium fugax*: Fox, 1983: fig.2), the hypoconulid is positioned directly posterior to the entoconid, while in *A. jasoni* (UALVP 2846, in which lower molars were found in occlusion with upper molars), the hypoconulid is more labially placed (**Figure 12B**). Setoguchi (1975, 1978, based on a suggestion by Robinson (1968), for insectivorans) suggested that the position of the hypoconulid in the herpetotheriines and other didelphids is associated with dilambdodont upper molars, without being more specific, or providing a functional reason why this should be so. This association is not evident in the lower molars of UALVP 2846. These lower molars were found in occlusion (Lillegraven, 1969) with upper molars (UALVP 2846, **Plate 12**) that are clearly dilambdodont, but the hypoconulid is not more posteriorly placed relative to the entoconid (**Figure 12C**), and is instead more labially positioned. The more posterior position of the hypoconulid relative to the entoconid in the herpetoteriines may instead be associated with the height of the metacone and the length of the premetacrista (Slaughter, 1968, 1971), rather than a dilambdodont morphology alone. The premetacrista shears against the postcristid of the lower molars (**Figure 7**), and as suggested in Chapter 2, changes in the length of one should be correlated with changes in the other. The postcristid runs posterolingually from the hypoconid to the hypoconulid, so that a shift in the hypoconulid to a more posterior position relative to the entoconid would increase the length of this postcristid. This could be associated with an increase in the length of the premetacrista and an increase in the height of the metacone, so that the relative sizes of the paracone and the metacone in the herpetotheriines could have been the result of a reduction in the paracone, but also an increase in the height of the metacone. These suggestions would be difficult to test empirically, and are meant only to serve as an illustration of the differences between *A. jasoni* and the herpetotheriines that can be examined through a consideration of the functional relationships of the upper and lower molars. Of course, the number of differences between two taxa are not as important phylogenetically as the synapomorphies they share, and in a cladistic analysis, similarities are originally postulated to be homologies. Homoplasy is revealed by the position of taxa on the cladogram, and therefore, the presence of dilambdodont upper molars in *A. jasoni* and *Peratherium* should be considered to be homologous (indicative of common ancestry between the two) until after the phylogenetic analysis has been performed. As discussed in Chapter 2, some researchers have recently placed an emphasis on improving character analysis in order to recognize homoplasy, prior to the phylogenetic analysis. Examining the functional relationships between upper and lower molars of *A. jasoni* and members of the Herpetotheriinae (*Peratherium*) is a means of recognizing possible homoplasy before the final cladogram is constructed. There are several differences in these functional relationships between these two taxa having to do with relative heights of the paracone and metacone, relative lengths of the crests constituting the centrocrista, and lengths of associated crests and positions of related cusps on the lower molars. Differences in these features, all related in some way to the centrocrista, suggest that *A. jasoni* is not closely related to members of the Herpetotheriinae, and that the presence of dilambdodonty in both is due to convergence. This morphology is not present within any other species referred to *Alphadon* s.l., except *Protalphadon* n. sp. A, in which the centrocrista was V-shaped and the valley between the paracone and metacone was deep, but the apex of the centrocrista did not reach the labial portion of the stylar shelf. The term "dilambdodont" was not applied to these upper molars. A further test of the relationship of *Alphadon jasoni* and members of the Subfamily Herpetotheriinae comes from the topology of the final consensus cladogram (**Figure 26**). In this cladogram, *A. jasoni* is separate from *Peratherium* (Subfamily

Herpetotheriinae), suggesting that the possession of dilambdodont is convergent in these two taxa.

In his revision of the Genus *Alphadon* s.l., Cifelli (1990a) named two new genera, *Turgidodon* and *Protalphadon*. Certain species previously assigned to *Alphadon* s.l.were referred to these two new genera, as reviewed earlier, and the remaining species, like *A. marshi* s.l and "*A. wilsoni*", remained in an unrevised *Alphadon* s.s. Cifelli (1990a: 298-299) states that *Turgidodon* and *Alphadon* s.s. differ from *Protalphadon* in the possession of more derived character states, for example, in the possession of a more consistently present stylar cusp C on the upper molars. However, *Alphadon* s.s. is not formally rediagnosed by Cifelli, and it is not stated which species are included in this taxon. Presumably these species would include those not assigned to *Protalphadon* and *Turgidodon*. Two of these taxa, *A. halleyi* Sahni, 1972 and *A. sahnii* Lillegraven and McKenna, 1986, are discussed below.

***ALPHADON HALLEYI* SAHNI, 1972 and *ALPHADON SAHNII* LILLEGRAVEN AND MCKENNA, 1986.** *Alphadon halleyi* and *A. sahnii* are two problematic species whose taxonomic status have been reviewed by several researchers (Lillegraven and McKenna, 1986; Montellano, 1986, 1988; Cifelli, 1990a), with little satisfactory resolution. Both species are assigned to the Judithian NALMA, and have been described from several formations across western North America. *Alphadon halleyi* is known from the Judith River (Sahni, 1972; Montellano, 1986) and the Two Medicine (Montellano, 1988) formations, both in Montana, the Oldman of Alberta (Fox, 1979a), the Kaiparowits of Utah (Cifelli, 1990a), and the lowermost Kirtland Shale of New Mexico (Rigby and Wolberg, 1987). *Alphadon sahnii* is known from the "Mesaverde" formation of Wyoming (Lillegraven and McKenna, 1986), the Oldman (as suggested by Lillegraven and McKenna, 1986, specimens previously referred to *A. halleyi* by Fox, 1979a), the Kaiparowits (Cifelli, 1990a) and possibly the Two Medicine formations (as suggested by Cifelli, 1990a, but contrary to Montellano, 1988). *Alphadon halleyi* and *A. sahnii* have been recognized from contemporaneous formations (Campanian in age), and from the same formations. This contemporeity of these two species and their morphological similarity has led to the recent taxonomic confusion. Specimens referred to *A. halleyi* have been removed to *A. sahnii* (Lillegraven and McKenna, 1986), and *A. sahnii* has been synonomized with *A. halleyi* (Montellano, 1986, 1988), but also maintained as a distinct species from *A. halleyi* (Cifelli, 1990a).

Alphadon halleyi was originally described by Sahni (1972), based on two lower molars (including the type specimen, AMNH 77367, a left m1), and a partial upper molar. Other researchers have assigned small numbers of specimens to this species, for example, Fox (1979) referred two lower molars and an M1, Lilllegraven and McKenna (1986) referred one lower premolar and five lower molars, and Cifelli (1990a) referred two damaged M1s and one lower molar. An important source of new information was given by Montellano (1986, 1988), who assigned 32 upper and 78 lower molars from the Judith River Formation (Hill County local fauna) to *A. halleyi*. Lillegraven and McKenna (1986) erected *A. sahnii* based on the holotype (UCMP 125337, an M1), and a large hypodigm (including lower molars, premolars and nine other upper molars), and suggested that this species was intermediate in size between "*A. wilsoni* " and *A. marshi* s.l. *Alphadon sahnii* was suggested to be most closely comparable to these latter taxa even though Lillegraven and McKenna (1986) removed an upper molar specimen assigned to *A. halleyi* and referred it to *A. sahnii*. Lillegraven and McKenna (1986) placed a great emphasis on the morphology of the premolars in the diagnosis of *A. sahnii*, suggesting that *A. sahnii* could be separated from other species of *Alphadon* s.l. on the basis of this premolar morphology.

Montellano (1986, 1988) suggested that specimens referred to *A. halleyi* and *A. sahnii* were closely similar in size, and that the only morphological difference between these two taxa was that on the one known M3 of *A. sahnii* (UW 17052, "Mesaverde" Formation, Wyoming), stylar cusp B was as tall as cusp C, while on M3s of *A. halleyi*, cusp C is smaller than cusp B. With regards to molar size, Montellano (1988), based on two fragmentary dentaries from the Two Medicine Formation and the larger Hill County local fauna (Judith River Formation), noted that the range of molar size variation for *A. halleyi* was greater than had been previously suggested (Lillegraven and McKenna, 1986), and that the lengths of m2 and m3 on the Two Medicine dentary (MOR 250) fell within the range of variation for *A. sahnii*, while the m1, if found isolated, would be referred to *A. halleyi* on the basis of size. Furthermore, there was no bimodality in molar measurements from the Hill County fauna that would suggest the presence of two separate species (*A. halleyi* and *A. sahnii*). Based on similarities in molar morphology, overlap in molar size, and lack of bimodality in molar size measurements, Montellano (1986, 1988) suggested that *A. sahnii* was based on larger individuals of *A. halleyi*, and therefore, *A. sahnii* was a junior synonym of *A. halleyi*.

Montellano did not consider the morphology of the upper premolars of *A. sahnii*, which made up a large part of the diagnosis of this species (Lillegraven and McKenna, 1986). This was one of Cifelli's (1990a) criticisms of Montellano's results; as well, Cifelli (1990a) suggested that the lack of a disjunct or bimodal size distribution in Montellano's sample could be due to the presence of *A. halleyi* in the Hill County local fauna and the absence of *A. sahnii*, rather than there being no significant size difference between the two. The first criticism is unwarranted since only one lower premolar (p3, AMNH 86343) has ever been referred to *A. halleyi* (Lillegraven and McKenna, 1986). As well, the morphology of this lower premolar agrees with some of the upper premolar character states given in the diagnosis of *A. sahnii*. These similarities include a lack of an anterior keel on the main cusp of the premolar assigned to *A. halleyi*, a lack of a basal cingula, and "obvious wear" only on the posterior keel of the main cusp (Lillegraven and McKenna, 1986: 30). In the diagnosis of *A. sahnii*, Lillegraven and McKenna (1986: 31-2) note "P2-3 usually lacking anterolingual parts of basal cingulum; P2-3 with anterior border of main cusp unkeeled and with strong wear on posterior crest of main cusp." Though there are similarities, this comparison was made between a lower premolar and upper premolars, and obviously, more premolars need to be assigned to *A. halleyi* before comparisons can be adequately made. It should be noted here that the only way any valid comparisons could be made between premolars of *A. sahnii* and *A. halleyi* would be by finding premolars in association with upper molars of *A. halleyi*, or preferably of **both** taxa. This is because unassociated premolars could be referred to *A. halleyi* either to prove (similar premolars) the synonomy with *A. sahnii*, or to disprove (dissimilar premolars) it. Since the association of molars and premolars is rare for Late Cretaceous marsupials (because of the mode of preservation, in terrestrial fluviatile deposits), the resolution of the synonomy of these two species should not rest on the morphology of the premolars, as was suggested by Cifelli (1990a). Because of these problems, and until associated dental elements for these species are found, it is preferable to base taxonomic comparisons for the most part on the morphology of the upper molars, and to try to resolve the synonomy of *A. halleyi* and *A. sahnii* on this basis.

Cifelli's second criticism, that there was no bimodality in Montellano's measurements simply because *Alphadon sahnii* was not represented at that locality could have some merit, but it is not clear why his statement is any more valid than Montellano's. Moreover, Cifelli (1990a: 310) states that in the samples from the Two Medicine Formation (and the Judith River Formation), measurements of *A. halleyi* show that this species is smaller than *A. sahnii* from the "Mesaverde" Formation, and that there is little overlap between the two. An examination of these measurements (Montellano, 1988: tables 2, 3) in fact shows that there is some overlap in length and width for the following teeth: m1, m2, m3, width of m4, and M2.The length (2.0mm) and width (2.7mm) of the only M3 referred to *A. sahnii* fall at the lower (2.0-2.3mm) and upper (2.2-2.7mm) ranges of *A. halleyi*, respectively. A further comparison requires more upper molar specimens of *A. sahnii*. Though there are a total of 26 M1-M3s measured for *A. halleyi*, there are only 8 for *A. sahnii*, and again, there is the problem of establishing appropriate size ranges for these two species that are said not to be readily separated by any other morphological criteria.

The taxonomic status of *A. halleyi* and *A. sahnii* is difficult to resolve given the specimens involved and the diagnoses and descriptions given for these two species. With regards to these specimens, both species have been described and separated from one another, and from other species of *Alphadon* s.l. primarily on the basis of dental elements other than the upper molars, including lower molars (*A. halleyi*) and premolars (*A. sahnii*). This is problematic because most other species of *Alphadon* s.l. have been described on and are well known from referred upper molars, which tend to show more morphological variation, and therefore have more taxonomic information, than lower molars or premolars. Lower molars referred to species of *Alphadon* s.l. are morphologically similar and difficult to distinguish on the basis of any feature other than size. As with *A. halleyi* (Sahni, 1972: 381), the more informative upper molars must then be referred on the basis of similarity in size to the lower molars (i.e., Sahni, 1972: 381). Recent referrals of upper molar specimens to *A. halleyi* and to *A. sahnii* make it possible to come to some sort of resolution as to whether these are two distinct species or one.

Upper molars have been variously referred to *A. halleyi* (Sahni, 1972; Fox, 1979a; Rigby and Wolberg, 1987; Montellano, 1986, 1988 and Cifelli, 1990a), and a revised diagnosis, based largely on upper molar features, is given by Rigby and Wolberg (1987). Unfortunately, the features given in this diagnosis are generally not exclusive to *A. halleyi* among species of *Alphadon* s.l. Montellano (1986) refers a large number of new specimens to *A. halleyi*, but retains the diagnosis given by Sahni (1972), as does Cifelli (1990a). Again, this diagnosis is not useful for separating *A. halleyi* from other species of *Alphadon* s.l. One character state noted in the description of Rigby and Wolberg (1987: 662), is that the metastylar wing is prominent on upper molars of *A. halleyi*. This implies that the metastylar wing or the posterior stylar shelf (or even the postmetacingulum) is more posterolabially directed, and are transversely wider than the anterior stylar shelf. This is clearly observed on the M1 assigned to this species by Sahni (1972: fig. 13W, **Plate 20A**), on UALVP 6987 (M1, Oldman Formation, subsequently referred to *A. sahnii* by Lillegraven and McKenna, 1986, **Plate 20B**), and the M1 referred by Rigby and Wolberg

(1987) to *A. halleyi* (UNM-B1742: **Plate 20C**), as well as on several molars assigned to *A. halleyi* by Montellano in the UCMP collections (personal observation). A more posterolabially directed stylar shelf was also observed on M2s and some M3s referred by Montellano to this species. Though the metastylar region is better developed on M1s referred to *Alphadon* s.l. generally, the postmetacrista becomes more labially directed and the posterior stylar shelf is less posteriorly directed and more equal in size to the anterior shelf on M2, and even more so on M3 (i.e., *A. jasoni*, **Figure 8**). The greater development of the posterior stylar shelf (or the metastylar wing) relative to the anterior shelf, and its greater labioposterior orientation on M2 and M3 of *A. halleyi* separate this species from most others referred to *Alphadon* s.l. Whether or not this includes *A. sahnii* is examined below. One character correlated with the narrower anterior stylar shelf is a more broadly open ectoflexus than on other M3s referred to *Alphadon* s.l., where the anterior stylar shelf is subequal in width to the posterior shelf, and the ectoflexus tends to be deeper and narrower (**Figure 8**).

Another feature characterizing specimens referred to *A. halleyi* is the position of the paraconule and metaconule relative to the protocone and the paracone-metacone. In *A. halleyi*, the conules are positioned closer to the protocone and so more separated from the paracone and metacone (Montellano, 1986), while in other species of *Alphadon* s.l., the conules are more closely approximated to the paracone and metacone. This state may not be found consistently within *A. halleyi*; for example, the conules in UNM-B1742 (**Plate 20C**) are placed closer to the paracone and metacone than to the protocone. These two character states are not placed in a revised diagnosis for *A. halleyi* because, although I was able to study Montellano's specimens and most specimens referred to *A. sahnii* (AMNH collections), I was not able to examine these as closely as an adequate revision (including full descriptions) would require. Therefore, this discussion will be limited to a comparison between specimens assigned to *A. halleyi* and *A. sahnii*, with regards to the characters mentioned above. A tentative revision will be suggested, limited to whether or not *A. sahnii* is a junior synonym of *A. halleyi*, and whether both should be coded in the following phylogenetic analysis.

Upper molars referred to *A. sahnii* (Lillegraven and McKenna, 1986) are few in number, with only two M1s (including the holotype, UCMP 125337), five M2s and one damaged M3 in the hypodigm. The figure of the holotype (Lillegraven and McKenna, 1986: fig. 13A) suggests that the posterior stylar shelf is well developed and posteriorly directed, though perhaps not as wide relative to the anterior stylar shelf as in M1s of *A.*

halleyi from the Hill County local fauna (Montellano, 1986: fig 12 a,b). The other M1 listed in the hypodigm of *A. sahnii*, AMNH 86337 was very damaged. The figured M2 (AMNH 108686) and other M2s examined (AMNH 86312, 86313, 108686, 86333) again show a well developed and posteriorly directed posterior stylar shelf, and a broadly open ectoflexus. The posterior stylar shelf is wider than the anterior stylar shelf. The one M3 in the hypodigm (UW 17052) is stored at the University of Wyoming, and was not available for examination. In the figure given for this specimen (Lillegraven and McKenna, 1986: fig. 13c), the postmetacrista appears directed posterolabially, and the posterior shelf also seems oriented in this direction, although to a lesser degree than on referred M1s and M2s. Therefore, at this point, it appears that upper molars referred to *A. sahnii* are similar to *A. halleyi* in the greater development and posterolabial orientation of the posterior stylar shelf, a character state said above to separate *A. halleyi* from other species referred to *Alphadon* s.l.

With regards to the position of the conules relative to the protocone and the paracone and metacone, my sketches and notes regarding specimens referred to *A. sahnii* suggest that the conules on these specimens are positioned closer to the protocone than to the paracone-metacone. This was not mentioned in the descriptions given by Lillegraven and McKenna, and is not observed in the specimens figured by Lillegraven and McKenna (1986). The variability of this character state within *A. halleyi* (as discussed above), and probably in *A. sahnii*, reduced the usefulness of this character state. It is mentioned as a potentially important character, perhaps when the morphological variation in these two species is better understood, but is not included here in the phylogenetic analysis.

Some problematic specimens have recently been referred to *A. sahnii* by Cifelli (1990a: fig. 8). These are OMNH 20114 and 20116, said to be an M2 and M3, respectively. On OMNH 20114, the anterior and posterior stylar shelves are equal in width, and the ectoflexus is deeper, a morphology that is generally not characteristic of M2s referred to *Alphadon* s.l. On OMNH 20116, the anterior shelf is narrower than the posterior, and the ectoflexus is shallow and broad, again, not generally characteristic of M3s referred to *Alphadon* s.l., but rather, M2s. Instead, these two specimens are more likely an M3 (OMNH 20114) and M2 (20116). An examination of OMNH 20114 (from available casts) shows that the paracone is larger than the metacone, both in height, and in the circumference of its base. This is an unusual condition for upper molars referred to any taxon in *Alphadon* s.l., and was not described within *A. sahnii* by Lillegraven and McKenna (1986). On OMNH 20114, stylar cusp C is slightly larger than D, which is similar to the morphology on the M3 assigned to *A. sahnii* by Lillegraven and McKenna (ibid.), but the unusual paraconal morphology suggests that this specimen should not be referred to *A. sahnii*. ONMH 20116, an M2, has a moderately deep ectoflexus and a well developed and posteriorly projecting posterior stylar shelf, similar to the morphology discussed above for M2s of *A. halleyi*. Cifelli also refers two upper M1s and a lower molar to *A. halleyi*, and the one cast available for examination (OMNH 20119, M1, **Plate 20D**) is similar in all respects to other M1s of *A. halleyi* described above, including others in **Plate 20**. Cifelli (1990a: 310) suggests that specimens from the Kaiparowits Formation support the distinctiveness of *A. halleyi* and *A. sahnii*, in that materials referred to *A. sahnii* are larger with relatively more robust cusps. The size comparison involves M1s referred to A. *halleyi* and M2s and M3s assigned to *A. sahnii*, and so less meaningful than if similar molars were being compared. As mentioned above, one of Cifelli's specimens (OMNH 20114) referred to *A. sahnii* should be removed and the presence of relatively more robust cusps in remaining specimens assigned to *A. sahnii* could certainly be due to individual variation. This specimen showed morpholgical similarity to *A. halleyi*, as discussed earlier. Therefore, Cifelli's Kaiparowits specimens do not necessarily support a separation of *A. sahnii* and *A. halleyi*, and *A. sahnii* is considered to be a junior synonym of *A. halleyi*, as suggested by Montellano (1988). *Alphadon halleyi* alone is coded in the upcoming phylogenetic analysis.

OTHER TAXA REFERRED TO *ALPHADON* S.L. Other taxa have been referred to *Alphadon* s.l., but were not extensively reviewed or revised in the previous parts of this chapter. These taxa are either described on the basis of poorly preserved specimens, on the basis of a small number of specimens, or almost exclusively on lower molars and premolars, all of which do not provide adequate information for distinguishing the taxon at the species level. The holotype of *Alphadon parapraesagus* Rigby and Wolberg, 1987 is a fragment of a lower mandible with m3-4 (UNM-B5538). This species would now be referred to *Turgidodon* because of its larger size and robust cusps. The hypodigm includes only one other specimen, a partial upper molar preserving the protocone, paracone and the anterior stylar cusps. In the diagnosis, *T. parapraesagus* is described as being morphologically similar to (lower molars of) *T. praesagus*, but differs in that the cristid obliqua of UNM-B5538 meets the posterior wall of the trigonid labial to the protocristid notch. This is unusual for lower molars referred to *Alphadon* s.l. because on these the cristid obliqua generally meets the posterior wall basal to or below the postcristid notch. Other diagnostic characters given for *T. parapraesagus* include a hypoconulid more closely twinned with the entoconid than posteriorly projecting, and a trigonid that is slightly shorter anteroposteriorly than that of *T. praesagus*. These latter two tend to be variable within taxa (Cifelli, 1990a) and along the tooth row, especially the anteroposterior length of the trigonid, which decreases from M1 to M3 on lower molars assigned to *Alphadon* s.l. Since only one lower molar specimen of *T. parapraesagus* is available for comparison, it is impossible to be certain whether these differences represent a species-level morpholgical gap, or if UNM-B5538 instead represents an upper range of values for *T. praesagus*. The position of the cristid obliqua on UNM-B5538 definitely separates this specimen from *T. praesagus*. Cifelli (1990a: 302) notes that this position of the cristid obliqua is more characteristic of lower molars referred to *Pediomys* and *Aquiladelphis*, but that an examination of the figured specimen does not support a referral of UNM-B5538 to either of these genera. Cifelli (ibid.) also notes that Rigby and Wolberg (1987) separate *T. parapraesagus* from *T. praesagus* by suggesting that in *T. parapraesagus* the metaconid is not smaller than the paraconid in occlusal view; this implies that the metaconid is smaller than the paraconid in *T. praesagus* which, as Cifelli (1990a) notes, is incorrect (for example, see Fox, 1979a: fig.1e-f, lower molars of *T. praesagus*). Cifelli states that the referred upper molar of *T. parapraesagus* might belong to *T. rhaister*, or a closely related species (also Rigby and Wolberg, 1987), but nevertheless retains *T. parapraesagus* and classifies it in his new genus, *Turgididon*. This referral is not followed here because of the morphology of the cristid obliqua of the holotype, and the uncertain identification of the single fragmentary upper molar. Until more specimens are formally referred to *T. parapraesagus* (i.e., those from the Hunter Wash local fauna (Clemens, 1973), suggested by Rigby and Wolberg (1987: 63) to be similar to *A. parapraesagus*), this species is considered to be a *nomen dubium*, and not included in the phylogenetic analysis.

Alphadon attaragos Lillegraven and McKenna, 1986 was described from the "Mesaverde" Formation, Bighorn Basin, Wyoming, the type and only known specimen of which was a isolated left m1. *Alphadon attaragos* was separated from all other species of *Alphadon* s.l. primarily by its small size, and by a more posteriorly positioned metaconid, relative to the protoconid, a conical (though damaged) hypoconulid, and sharp, uninflated molar cusps. As noted above, m1s assigned to *Alphadon* s.l. have a relatively wider trigonid (paraconid and metacond more widely separated) than m2s and m3s. Therefore, it is not surprising that the metaconid is more posteriorly placed on the m1 referred to *A. attaragos*, and a comparison in this character between *A. attaragos* and other species of *Alphadon* s.l. requires more specimens. Lillegraven and McKenna (1986) note that the single lower molar referred to *A. attaragos* does not provide adequate information for the reconstruction of phylogenetic relationships to other taxa. They further note that this lower molar is similar to those referred to *A. sahnii*, and *A. attaragos* may represent a smaller individual of *A. sahnii*. The measurements given for the lower molar of *A. attaragos* are much smaller than those given for *A. sahnii*, but the importance or significance of this difference again requires an examination of more specimens referred to *A. attaragos*. Montellano (1988) referred additional lower molars to *A.* cf. *A. attaragos* on the basis of size similarities to the holotype, but noted that the metaconid was not as posteriorly displaced on these specimens. My own notes on these specimens state that the cristid obliqua is more labially placed and does not meet the posterior wall of the trigonid basal to the protocristid notch as in other lower molars referred to *Alphadon* s.l. Therefore, these specimens may not be referable to *A.* cf. *A. attaragos* or even *Alphadon* s.l.

Cifelli (1990a) referred upper molar specimens to *A. attaragos* from the upper Kaiparowits Formation of Utah (roughly contemporaneous to the "Mesaverde"), including additional lower molars and two upper molars. These lower molars include a m1, which Cifelli (1990a) refers to *A. attaragos* with little question. Upper molars are referred on the basis of similarities in size to both the type specimen and the m1 from the Kaiparowits Formation. The description of the fragmentary M1 (OMNH 20152, **Plate 20E**) suggests few morphological differences from any other M1 referred to *Alphadon* s.l., except that stylar cusp B is said to be nearly equal in height to the paracone (ibid.: 314). This feature is otherwise restricted to species referred by Cifelli to the Genus *Turgidodon*, including *T. russelli*, *T. praesagus*, and *T. rhaister*. This is also the case for the referred M2 (OMNH 20147). Upper molars of *A. attaragos* are smaller and less robust those of any species referred to *Turgidodon*, so that the subequal protocone, paracone and stylar cusp B are more likely convergent in these taxa. Cifelli (1990a) also describes the labial faces of the paracone and metacone as flat to concave, but an examination of a cast of this specimen does not support this statement. Other characters given in the description for OMNH 20147 (M2) are seen throughout *Alphadon* s.l., except possibly the close approximation of stylar cusps C and D. This is also seen in some specimens of *Turgidodon praesagus*. One cast was available for examination (OMNH 20152), the M1, and a camera lucida drawing of this specimen was included in **Plate 20** to show that this upper molar is similar in general morphology to M1s of *A. halleyi*, particularly in the shape of the stylar shelf. One difference between these specimens is that stylar cusp C is larger in OMNH 20152 (**Plate 20E**) than on the other upper molars (all M1s) on **Plate 20**. Whether this is a species-level difference, or whether OMNH 20152 should be referred to *A. halleyi* cannot be determined with the small number of specimens available for both taxa. With more material, it may be discovered that *A. attaragos* is most closely related to *A. halleyi*, which would be valuable knowledge given the level of resolution of taxa previously referred to *Alphadon* s.l. in the final cladogram (**Figure 26**). As both Lillegraven and McKenna (1986) and Cifelli (1990a) note, the use of finer mesh screens in washing collected sediments will result in smaller specimens, like those referred to *A. attaragos*, being collected.

Alphadon attaragos is separated from other species referred to *Alphadon* primarily on the basis of the small size of the referred molars. Molar size is not included as a character in the phylogenetic analysis because of the difficulties in transforming quantitative characters (measurements) into qualitative ones (each state given a integer value; 0, 1, 2...). Even if molar size was included, the state for *A. attaragos* ("extremely small") would be an autapomorphy for this taxon, and would not be included in the analysis. Autapomorphies increase the length of the cladogram without providing information regarding relationships to other taxa, and so are excluded. Therefore, *A. attaragos* is not included in the phylogenetic analysis.

CHAPTER 4

PHYLOGENETIC ANALYSIS

The methods of phylogenetic analysis were described in Chapter 2, including the various outgroups and more derived ingroup marsupial taxa used. Taxa referred to *Alphadon* s.l. were reviewed and revised in Chapter 3. Certain species referred to this genus are not included in this analysis, for reasons given in this latter chapter. The character and character states used are described in detail below, and the data matrix is presented following this discussion.

CHARACTERS AND CHARACTER STATES

STYLAR CUSPS

The stylar cusps are situated along the stylar shelf, and have been variously designated, with the nomenclatural system for marsupials accepted today being that of Simpson (1929: fig. 43B-F, with modifications by Clemens, 1966). In this system, restricted to marsupial taxa, the cusps are designated by capital letters, from A, the most anterior stylar cusp, through to E, the most posterior. Stylar cusps in other mammalian taxa are referred to by certain names, for example, parastyle, stylocone, and metastyle. As Butler (1978: 451) notes, names applied to molar cusps imply certain topographical relationships to other cusps, as well as functional relationships with cusps on opposing (or lower) molars. Both relationships are used to assess cusp homologies between taxa, and are applied to the homologies of stylar cusps between the marsupial taxa examined here and the various outgroups (Eutheria, Deltatheroida, *Pappotherium*). Inferences of stylar cusp homology have been discussed by several authors, including Cope (1893), Osborne (1888b), Bensley (1903), Patterson (1956), and Clemens (1966, 1979). It is generally agreed that stylar cusps A and B are homologous, when present, in marsupials and placentals, such that cusp A is homologous with the parastyle and cusp B with the stylocone. The assessment of the homology between cusp B and the stylocone was made on the basis of a consideration of the function of these cusps among the various taxa. Patterson (1956) noted that stylar cusp B and the stylocone both were labially positioned relative to the paracone and connected to this cusp by a long crest (the preparacrista), that sheared against the paracristid of the lower molars. In this way, both function and topology of the stylar cusps were used to determine homology. As well, both the parastyle and stylar cusp A are positioned anterior to the stylocone (cusp B), with an anterior cingulum running lingually from the parastyle/cusp A to the preparaconular crista and the paraconule. This cingulum also shears against the paracristid, but may not be complete in all taxa. This would not, however, change the implied homology between the parastyle and stylar cusp A.

The homologies of stylar cusps C and D are more difficult to illustrate, and depend less on functional relationships than topology. This is because the functions of stylar cusps C and D in the chewing cycle are difficult to ascertain, as discussed in Chapter 3. Therefore, homologies between cusps C and D and cusps in the various outgroup taxa used here depend on the position of these cusps, often relative to one another, the ectoflexus, and the metacone. In this analysis, stylar cusps of marsupial and outgroup taxa will be considered homologous (both presence and absence) as an original hypothesis, based on morphological similarity. An excellent example involves the homology between stylar cusp D in marsupials and similar cusps in the outgroup taxa. For the marsupial taxa examined here, stylar cusp D is positioned posterior to the deepest part of the ectoflexus and stylar cusp C (if present), while being labial to the metacone. A small cusp in these relative positions is also observed in *Prokennalestes* (Kielan-Jaworowska and Dashveg, 1989; figs. 5, 7, 11, 12, 13, 14), in *Kennalestes* (Kielan-Jaworowska, 1968; fig. 2A, 2B; Clemens and Lillegraven, 1986: 63), and in *Pappotherium* (personal examination of a cast of the holotype). This cusp appears well developed in *Prokennalestes* but less so in *Kennalestes* and *Pappotherium*. On the holotype of *Pappotherium pattersoni* (**Figure 10B**), this small cusp is associated with smaller cuspules. Clemens and Lillegraven (1986: 78) note that if the presence of a small stylar cusp D is considered to be a synapomorphy of the Marsupialia, then other non-marsupial taxa like *Kennalestes* and *Pappotherium* (and other tribosphenic and nontribosphenic taxa) would have to be referred to the Marsupialia, which is not supported by other characters. Therefore, they suggest that the presence of a cusp in the region of stylar cusp D arose separately in the marsupials and in these other taxa, or in other words, that the presence of a cusp in this region is not homologous among these taxa. The argument presented by Clemens and Lillegraven (1986) seems to revolve around the suggestion that stylar cusp D is a synapomorphy for the Marsupialia, and that since this is so, cusps in a similar position on the stylar shelf of eutherians and other tribosphenic therians cannot be homologous to stylar cusp D. The definition of homology used in this analysis revolves around similarity (at least as an initial hypothesis), including similarity in position on the molar occlusal surface. Therefore, the small cusp observed on upper molars of *Prokennalestes*, *Kennalestes* and *Pappotherium* is considered to be homologous to stylar cusp D of the marsupials, because of similarities in position relative to the ectoflexus and metacone.

In the interest of saving space and avoiding repetition, the stylar cusp characters described below will use the terminology appropriate for the Marsupialia, with homologies of these cusps to cusps in outgroup taxa as described above. Dental homologies were discussed in Chapter 2, and when necessary, terms like "penultimate" molar and "anteriormost to posteriormost" molar will be used. For the marsupials, these terms would correspond to M3/3 and M1/1-M3/3, respectively. Most of the dental characters discussed below involve structures that are generally considered to be homologous between the Marsupialia and the various outgroup taxa (i.e., paracone, metacone, protocone, conules).

STYLAR CUSP A (parastyle)

1) size: this cusp is situated on the parastylar lobe and can be either relatively small (**state 0**) or large (**state 1**) in size.

2) position relative to stylar cusp B: cusp A may be more closely approximated to cusp B such that cusp A is approximately at the same level of the stylar shelf as cusp B (**state 0**) or stylar cusp A will be lower and more basally placed relative to B (**state 1**).

STYLAR CUSP B (stylocone)

3) Size: stylar cusp B is the largest stylar cusp on the stylar shelf (**state 0**) but may be hypertrophied (**state 1**), or smaller and more nearly equal in size to cusps C and D (**state 2**).

4) Height of B relative to the paracone (PAC) and the protocone (PRC): cusp B can be shorter and smaller (**state 0**) or it can be more nearly equal in height to both due to an overall lowering of molar cusps (**state1**).

PREPARACRISTA

5) Strength of crests contributing to the preparacrista (PPCR) from the PAC and cusp B: these crests can be equal in strength so that the crest from cusp B is easily seen in occlusal view and extends to the apex of cusp B (**state 0**) or this crest may be weak and more difficult to see in occlusal view (**state 1**).

STYLAR CUSP C (mesostyle)

6) Presence or absence: stylar cusp C is either absent (**state 0**), variably present (**state 1**), consistently present (**state 2**), or present as two small cuspules (**state 3**).

Taxa that were coded state 0 for character 7 above are coded as state 9 ("missing") for characters 8- 12.

7) Position of cusp C relative to the ectoflexus: cusp C can either be placed at the deepest part of the ectoflexus (**state 0**) or anterior to the deepest part of the ectoflexus (**state 1**).

8) Position relative to the labial edge of the stylar shelf: cusp C can either be placed along the labial edge of the stylar shelf (**state 0**), or can be more lingually placed (**state 1**), or extremely lingually placed, closer to the labial base of the paracone (**state 2**).

9) Orientation of stylar cusp C relative to the edge of the stylar shelf: stylar cusp C can either, as determined from the position of crests from the apex of this cusp, be oriented antero-posteriorly (**state 0**) or anterolingually-posterolabially (**state 1**).

10) Size of C relative to D on penultimate molar: cusp C can be smaller than D on penultimate molar (**state 0**) or cusp C can be larger than D (**state 1**).

11) Cusp C shape in labial view: cusp C can be conical (**state 0**) or squared at its apex (**state 1**).

STYLAR CUSP D (homologies as discussed above)

12) Presence or absence: stylar cusp D can either be absent from the posterior portion of the stylar shelf (**state 0**) or it can be distinctly present (**state 1**).

STYLAR SHELF

13) Anterior width relative to posterior width on penultimate upper molar (M3/ for the Marsupialia): the anterior shelf may be as wide as the posterior shelf (**state 0**) or it may be narrower than the posterior shelf (**state 1**).

POSTMETACRISTA

14) orientation: the postmetacrista may be oriented labially (**state 0**) or more posterolabially (**state 1**).

ECTOFLEXUS

15) upper molar trends in size and shape: the ectoflexus may be deeper on all upper molars (**state 0**), or shallower on the anterior molars and increasing in depth posteriorly (M1/-M3/ for the Marsupialia, **state 1**), or the ectoflexus may be shallow on all upper molars (**state 2**).

PARACONE AND METACONE

16) Relative height: the PAC may be taller than the metacone (MEC) (**state 0**), the PAC and the MEC may subequal in height (neither distinctly or consistently taller than the other, **state 1**) or the MEC may be taller than the PAC (**state 2**).

17) Relative sizes in labial view: In labial view, the labial side of the tooth is held towards the observer so that the labial edge of the stylar shelf and the labial sides of the paracone and metacone are visible. In this view, the PAC and the MEC may be of equal size (each measured anteroposteriorly, **state 0**), or the MEC may be larger (broader anteroposteriorly) than the PAC (**state 1**), or the PAC may be larger than the MEC (**state 2**).

18) Shape and absolute sizes: the PAC and the MEC may be uninflated and less rounded (**state 0**), or they may be more rounded and conical (**state 1**).

19) Connate at bases: the PAC and MEC may be connected at their bases and for a certain portion of their heights (connate, **state 0**), or they may be entirely separate (**state 1**).

20) Relative separation: the PAC and MEC may be closely spaced on the molar (**state 0**), or they may be more widely separated (**state 1**).

21) Shape of labial faces: the labial faces of the PAC and the MEC may be rounded and more inflated (**state 0**), or they may be flat to concave (**state 1**).

22) Lingual extent of the bases: the base of the PAC may extend more lingually than that of the MEC (**state 0**), or the bases of the PAC and MEC may be approximately equal in labial extent (**state 1**).

CENTROCRISTA

23) Shape: the centrocrista may be straight (predilambdodont or rectidont; Van Valen, 1988, **state 0**), or V-shaped, with the apex reaching the lingual side of stylar cusp C, and the valley between the paracone and metacone broad and shallow (**state 1**). The apex of the centrocrista may be U-shaped and directed towards but not reaching the row of stylar cusps (**state 2**), or the apex may be U-shaped as well as reaching the level of the stylar cusps (dilambdodont, **state 3**).

CONULES

24) Size: the metaconule (METACON) and the paraconule (PARACON) can be smaller and weakly developed (**state 0**), or larger and more strongly developed (**state 1**), or the paraconule may be reduced in size relative to the metaconule (**state 2**).

25) Strength, morphology of the internal cristae: The internal cristae are the crests that run labio-internally from the PARACON and the METACON to the bases of the paracone and metacone. These crests may be absent (**state 0**), weak and low (**state 1**), more strongly developed (**state 2**), or represented by high, wall-like structures that are less crest-like (**state 3**).

PROTOCONE

26) Length anteroposteriorly: This character actually describes the width of the protocone (PRC) except that in keeping with the generalized measurements of the therian upper molar (**Figure 2**), the protocone is measured in an anteroposterior direction. The PRC may be shorter anteroposteriorly (PRC compressed, **state 0**), or it may be anteroposteriorly longer (**state 1**).

27) Basal posterior expansion: The basal posterior portion of the PRC may be unexpanded (**state 0**), or this portion may be expanded so that this part of the protocone is lobe-like (**state 1**).

28) Position relative to the PAC: the PRC may be positioned further posteriorly relative to the PAC (**state 0**), or positioned further anteriorly so that the PAC and the PRC are approximately in line (**state 1**).

29) Presence or absence of PRC cingula or rugosities: These rugosities or cingula are found along the sides of the PRC, and may be entirely absent (**state 0**), or be found only on the posterior side of the protocone, or on both the anterior and posterior sides of the protocone (**state 1**).

TRIGON BASIN

30) Depth: the trigon basin may be deep (**state 0**), or it may be shallow (**state 1**).

PREPARACINGULUM

31) Strength of preparacingulum from paraconule to stylar cusp A: the preparacingulum may not be continuous, or interrupted at the level of the PAC (**state 0**), or the preparacingulum may run continuously from the PARACON to stylar cusp A (**state 1**). The preparacingulum corresponds to shearing surface 1b in the terminology developed by Crompton (1971).

POSTMETACINGULUM

32) Presence or absence: the postmetacingulum may be present (**state 0**) or reduced to absent (**state 1**). The postmetacingulum corresponds to shearing surface 2b in the terminology of Crompton (1971)

LOWER MOLARS

Fewer characters are recovered from the lower molars than from the upper molars. Some reasons for this disparity have been discussed in Chapter 2, and characters listed here generally reflect morphological differences at the generic level. One concern discussed in Chapter 2 involved coding repetitive characters from functionally related features on upper and lower molars. Where possible, a short statement identifies these characters below.

TRIGONID AND TALONID

33) Relative widths on all but the ultimate molar: the talonid can be narrower (**Figure 2b**) than the trigonid (**state 0**), or the talonid and trigonid can be of equal width (**state 1**).

34) Relative heights: when the lower molar is held approximately horizontally, the talonid can be lower than the trigonid (**state 0**), or the talonid can be closer to the trigonid in height (**state 1**).

ENTOCONID

35) Shape: the entoconid (ENTCD) can be broader in an anteroposterior direction (**state 0**), narrower (**state 1**), or "spire-like" (Crochet, 1979, 1980; **state 2**).

ENTOCONID AND HYPOCONULID

36) Relative sizes: the ENTCD and the hypoconulid (HYPCLD) may be subequal in height (as measured from the base of crown, **state 0**), the ENTCD may be taller than the HYPCLD (**state 1**), or the HYPCLD may be larger (**state 2**).

37) positions of the hypoconulid relative to the entoconid relative to the hypoconid (HYPCD; this character may be related to the relative height of the MEC): these three cusps may be equally spaced on the talonid (**state 0**) or the HYPCLD may be more closely approximated to the ENTCD and positioned further from the HYPCD (**state 1**).

38) position of the hypoconulid relative to the entoconid (this character may be correlated with the relative sizes of the PAC and MEC): the HYPCLD may be more labioposteriorly placed relative to the ENTCD (**state 0**), or the HYPCLD may be more posteriorly placed so that the HYPCLD is more directly posterior to the ENTCD (**state 1**).

CRISTID OBLIQUA

39) Position at which the cristid obliqua meets the posterior trigonid wall (this character may be correlated with the height of the PAC): the cristid obliqua may meet the posterior wall of the trigonid at a point lingual to the protocristid notch (**state 0**), basal to the protocristid notch (**state 1**), or the cristid obliqua may meet the trigonid wall labial to the protocristid notch (**state 2**).

DISTAL METACRISTID

The distal metacingulid is a crest running labioposteriorly from the apex of the metaconid towards the talonid basin (Fox, 1975).

40) Distal metacingulid present or absent: The distal metacristid is present (**state 0**) or absent (**state 1**).

PREMOLARS

41) Number, in the generalized (primitive) dentition: the number of premolars may be five (**state 0**), four (**state 1**) or three (**state 2**).

42) General morphology (after Cifelli, 1990a): less robust and less bulbous (**state 0**) or more robust and more bulbous (**state 1**).

MOLARS

43) number, in the generalized (primitive) dentition: the number of molars may be three (**state 0**) or four (**state 1**).

DATA MATRIX

	[1234567890123456789012345678901234567890123]
Kennalestes	1030009999910010000000120011111110190001100
Prokennalestes	1000009999910010000000000001011000010001000
Pappotherium	1000009999910090200000000000011110110001100
***Protalphadon* n. sp. B**	1100009999910090001000001000001099999999101
Alphadon marshi	1100020100010011111101112100001011001011201
Alphadon jasoni	1100021100010011111111312100001011001011201
Alphadon halleyi	1100020110011101111101012100101011001011201
Alphadon creber	1000100000001001111001001000001010001011201
Alphadon* sp., cf. *A. creber	1100010000011001111001001000001010001011201
Protalphadon lulli	1100011000010010001001011000001110001011201
***Protalphadon* n. sp. A**	1100011000010010001011211000001110001091201
Turgidodon russelli	1112120111110011111101013110111011001011211
Turgidodon praesagus	1112120110110011111101013110111011001011211
Turgidodon rhaister	1112021200110011111101013110111011001011211
Turgidodon madseni	1102020001010021111101013100001011001011211
Turgidodon lillegraveni	1112120100010001211101013100111011001011211
Deltatheroida	0000009999900100000000000000000100100000201
Peradectes	0020020000010022101101012100001110101021201
Peratherium	0020020000011122111111312101011111211121201
Ankotarinja	0020030000010122111111322101011111211121201
Andinodelphys	0000030000011092101001021001001111121021201

RESULTS

This phylogenetic analysis was done in two phases. In the first of these, the data set presented above was run on the "heuristics" program available in PAUP 3.0 (Swofford, 1990). This is only an approximate algorithm, but runs very quickly, and gives results that will be close to the results obtained by the "branch and bound" or "exhaustive search" programs, which are guaranteed to find all minimal length cladograms. The heuristics program was used in order to make an initial assessment of the relationships of the taxa being examined; it was also used to see if there was any appreciable difference in using a data set in which all characters were unordered and one in which two characters were ordered (as discussed in Chapter 2). With heuristics, the data set was run with the multistate characters totally unordered; there was no *a priori* hypothesis about the order of the states in these characters. The branchswapping, nearest neighbour interchange method was used. The results of this run were 113 equally minimal length cladograms with length, 107 and a consistency index (C.I.) of .561. Since no actual ancestral taxa, and no specific ancestor- descendant relationships were included in this analysis, it is more appropriate to refer to the branching diagrams as cladograms. A strict consensus cladogram produced from these minimal length cladograms is shown in **Figure 21**. It would be an exceedingly complex task to evaluate 113 separate minimal length cladograms, and consensus cladograms are used as a summary of the topologies of these multiple equal length cladograms. As Anderberg and Tehler (1990: 401) note, the consensus cladogram recognizes only those components (or clades) that are **unequivocally** supported by the data. The strict consensus cladogram retains only those components which are present in all equal length cladograms, but there are various other types of consensus cladograms available. The Adams (Adams, 1972) and semistrict (Swofford, 1990; = combinable components; Bremer, 1990) consensus cladograms are described further below.

There is considerable resolution of the taxa on the strict consensus cladogram in **Figure 21**, but species referred to *Turgidodon*, *Alphadon halleyi*, *Alphadon creber* s.s., *Alphadon* sp., cf. *A. creber*, *A. jasoni*, *A. marshi*, and the clade including the more derived marsupial taxa form a major polytomy. After these cladograms were obtained, an option in PAUP 3.0 was used that reweights characters relative to their consistency indices, that is, relative to their degree of homoplasy on the initial cladograms obtained. This is the "successive approximations" approach, first described by Farris (1969). The successive approximations approach avoids the *a priori* weighting of characters, but allows the user to give more phylogenetic weight to characters that have been shown to be more useful in determining these phylogenies (the less homoplasious characters). Carpenter (1988) advocated the iterative use of successive approximations weighting through various runs, until additional weighting produces no fewer cladograms, rather than combining the original equal length cladograms into a consensus cladogram. In other words, an initial analysis produces cladograms, the characters are reweighted, then a new set of cladograms is produced. The characters are again reweighted on the basis of the second set of cladograms, new cladograms produced, the characters reweighted, etc. Because the less homoplasious characters (relative to their distribution on each successive set of cladograms) are given an increasingly greater weight in subsequent analyses, the number of cladograms produced will eventually decline. Carpenter (1988) has suggested this method be used because any of the original cladograms or those obtained through successive reweighting of characters will have a greater resolution than a consensus cladogram (which will tend to show more polytomies; also Miyamoto, 1985). Though Carpenter's suggestions have some merit, they are not employed here. Reweighting characters as he suggests will always approximate a clique methodology (LeQuesne, 1972), in which characters that are consistent with other characters are the only ones retained and used. An inital use of the successive approximations approach method still retains the "poorer" characters in the analysis (but gives them a lower taxonomic weight in a subsequent analysis), and therefore, no information is entirely excluded, as it is using clique methods.

The results of this second run employing the reweighted characters are shown in **Figure 22.** This is a strict consensus cladogram of the 34 equally minimal length cladograms found (length, 617, C.I., .669). The increase in the consistency index for this run is due to greater weight given to the characters that are less homoplasious, and the increase in length is due to the fact that when characters were reweighted, they were reweighted to a base of 10 (the reweighting option in PAUP allows for characters to be reweighted to a base of 1, 10, 100, 1000, etc.; these higher bases will give proportionately higher weights to the less homoplasious characters). Reweighting characters to a base of 1 results in characters with a C.I. of less than a certain value being reweighted as 0, while characters with a C.I. greater than this value were reweighted as 1.0. Reweighting to a base of 1 was not employed for the reasons just described above, in conjunction with clique methods. The consensus cladograms in **Figure 22** are similar to the strict consensus cladogram produced with the unweighted data (**Figure 21**), but the resolution is improved. *Alphadon creber* s.s. and *Alphadon* sp., cf. *A. creber* are now positioned outside the polytomy described above (*Turgidodon*, *Alphadon halleyi*, *A. jasoni*, *A. marshi*, and the more derived marsupial taxa), and as a polytomous clade themselves, are the sister group to these taxa. This is not unexpected, given that *A. creber* s.s. and *Alphadon* sp., cf. *A. creber* are characterized by the variable presence of stylar cusp C, while the taxa in the larger polytomy possess a distinct and consistently present cusp C. The two species referred to *Protalphadon* are also resolved as a polytomy, and are the sister group to the taxa just discussed. *Protalphadon* n. sp. B (included specimens formerly referred to *Iqualadelphis lactea* by Cifelli, 1990a) is the next less inclusive sister taxon.

A third and fourth run were performed in which two of the multistate characters were designated as ordered. These were character **16**, the relative sizes of the paracone and metacone, and character **39**, the position of the cristid obliqua at the posterior wall of the trigonid. These characters are functionally related to one another, as discussed in Chapter 2, and therefore, both should be ordered in the analysis. The states for character **16** are as follows: state 0- paracone larger than the metacone; state1- paracone and metacone subequal in size (neither distinctly or consistently taller than the other); state 2- metacone larger than the paracone. The states for character **39** are: state 0- cristid obliqua meets the posterior wall of the trigonid at a point lingual to the protocristid notch; state 1-cristid obliqua meets the trigonid wall basal to the protocristid notch; or state 2- cristid obliqua meets the trigonid wall labial to the protocristid notch. The ordering of these characters suggests that in the transformation series for both characters, state 1 is between states 0 and 2, but no direction is implied. In the third run, characters **16** and **39** were ordered, but there was no *a priori* weighting of any characters. The resulting strict consensus cladogram does not differ in any way from the strict consensus cladogram produced from the unordered and unweighted data (**Figure 21**).

After this third run, the characters were reweighted, as described above. These new data were analyzed in the fourth run, giving 34 minimal length cladograms (length, 617, C.I., 669). Again, the strict consensus cladogram produced shows no difference in distribution of taxa from the strict consensus cladogram produced from the unordered, reweighted data (**Figure 22**). These results suggest that the information regarding the ordering of certain characters does not alter the phylogenetic relationships suggested by the unordered data (at least in this analysis), and the data set including these two ordered characters will be used in the "branch and bound" method of phylogenetic analysis, but the entirely unordered data set will not. The branch and bound methodology was originally described by Hendy and Penny (1982), and, as mentioned above, is guaranteed to give all minimal length cladograms. Swofford (1990), in his liner notes for PAUP 3.0, warned that for data sets with more than 10 taxa, the branch and bound method may take a long time (he was correct; this analysis with 21 taxa ran on a Macintosh LC computer for 33 hours), and that with 20 or more taxa, the exhaustive search method would be nearly impossible to complete. Since both methods give all possible minimum length cladograms and the exhaustive search method would be difficult to use for 21 taxa, the branch and bound method was the only one employed. Swofford (1990) also noted that these two methods are alternatives, without explicitly stating that the exhaustive search is superior to the branch and bound methodology.

Again, two runs were performed with the branch and bound method, an initial run with the ordered but unweighted data, producing 141 minimal length cladograms (length, 107, C.I., .561). This method found 28 extra minimal length cladograms in comparison to the heuristics method, but these cladograms did not decrease in length. In the second run, the characters were reweighted, producing 36 minimal length cladograms (length, 638, C.I., .669). In addition to the strict consensus cladograms, semistrict and Adams consensus cladograms were produced, in order to examine how different consensus methods would alter the resolution of relationships of the relevant taxa. In PAUP 3.0, four types of consensus cladogram may be constructed, including strict, semistrict, Adams and majority rule (Swofford, 1990). With majority rule, a consensus cladogram can be constructed from a certain percentage of cladograms that have a similar topology. This methodology ignores cladograms that do not have this topology (but which are equally well supported by the data), and therefore dismisses data, which would bias the final results (i.e., the final classification). For this analysis, the majority rule consensus cladogram was not found, but the other three types of consensus cladograms were, when possible. For the ordered but unweighted data, the strict and semistrict consensus cladograms are given in **Figures 23** and **24**, respectively. For the ordered and reweighted data, these two consensus cladograms and an Adams consensus cladogram are presented in **Figures 25, 26,** and **27**, respectively. An Adams consensus cladogram could not be obtained from the 141 equal length cladograms produced from the ordered and unweighted data set, even after the computer worked overnight.

Both the semistrict and Adams consensus cladograms shown in these figures are better resolved than the strict consensus cladograms with regards to *A. halleyi*, *A. jasoni* and *A. marshi*, and the semistrict consensus cladogram is better resolved with respect to *Protalphadon lulli* and *Protalphadon* n. sp. A. Bremer (1990) developed the combinable components or semistrict method for deriving consensus cladograms by noting that strict consensus cladograms contain only those components (or clades) occurring in **all** of the original cladograms. The semistrict method increases resolution by adding components which are present in some, but not necessarily **all** original cladograms, and that do not **conflict** with components occurring in the original cladograms. In the Adams consensus method (Adams, 1972), components not occurring in all original cladograms are resolved by grouping these at the node representing the last common ancestor of the taxa in these components, or as Bremer (1990: 370-1) notes, this methods works by "pulling down unstable taxa and components with different positions in the cladograms to the first node summarizing the different positions.". The Adams method has been criticized recently because it will include components that are not combinable with components in the multiple original cladograms (Bremer, 1990) or because it can include components not found in any of these original cladograms (Anderberg and Tehler, 1990). These criticisms were found to be true for the Adams cladogram obtained for the ordered and reweighted data set (**Figure 27**). Of the 36 original cladograms, the Adams consensus cladogram was found to have components (the component including *A. marshi*, *A. jasoni* and *A. halleyi*), in conflict (or to not be combinable) with 11 of these. Mickevich and Platnick (1989: 46) endorsed the Adams consensus method, because in finding a cladogram with the greatest amount of information (in terms of the numbers of components (clades) produced, and the number of terminal taxa included in these components), the Adams cladogram "combines all, rather than some, of the taxonomic statements found in common", as compared to the strict consensus cladogram, which combines only those taxonomic statements found in all equal length cladograms. Thus, the Adams consensus cladogram would have a greater amount of taxonomic information. While this may be the case, the Adams cladogram may still produce components not found in all original cladograms, which would seem to defeat the purpose of producing a consensus cladogram as a summary of taxonomic information in the first place. Because of these problems, the Adams consensus cladogram was not retained, and was not used to construct the final classification.

The semistrict consensus method was criticized by Anderberg and Tehler (1990) for the same reasons as the Adams method, that it produces components not found in all original cladograms. This may be the case, but if these additional components do not **conflict** with any of the components found in the original cladograms, and increase the resolution among the taxa, it seems that this is the preferable method for producing a consensus cladogram for the final classification. As Bremer (1990) suggests, not finding these additional combinable components is in fact, a loss of information. The semistrict consensus cladogram obtained from the 36 cladograms produced from the ordered and reweighted data set differs little from the strict consensus cladogram obtained. The only differences are that in the semistrict consensus cladogram, *A. marshi* and *A. jasoni* are resolved as sister taxa, while in the strict cladogram they are part of the polytomy along with *Turgidodon*, *Alphadon halleyi*, and the clade including the more derived marsupial taxa, and that in the semistrict consensus cladogram, *Protalphadon lulli* and *Protalphadon* n. sp. A are sister taxa, but in the strict consensus cladogram, they are not. The semistrict consensus cladogram of 36 equal length cladograms (**Figure 26**) produced by the branch and bound methodology from the data set in which characters 16 and 39 were ordered, and the entire data set reweighted using the successive approximations methodology of Farris (1969), is the cladogram used to construct the final classification in Chapter 5. Anderberg and Tehler (1990) note that the consensus cladogram should be used in construction of a classification, rather than any of the multiple equal length cladograms. This is because a classification based on one of these equal length cladograms will be in conflict with a classification based on any of the other equal length cladograms. The suggestions of Anderberg and Tehler (1990) have merit and are followed in this analysis.

Before the final classification is produced, the distribution of characters states must be examined. Miyamoto (1985), though criticizing the use of consensus cladograms obtained from multiple data sets, makes an important point regarding the relationship between the original data set, the cladograms produced from these data, and the consensus cladogram obtained from these (minimal length) cladograms. He (ibid: 187) notes that "consensus cladograms are generated from fundamental cladograms instead of original information", and that consensus cladograms do not represent parsimonious resolutions of the original data set. Miyamoto (ibid) provides an example where consensus cladograms require more character state changes or "steps" than does a cladogram produced from the same data. This may be due to the increase in homoplasy that occurs when taxa are placed in polytomies. In **Figure 28**, two sets of minimal length cladograms (A1, 2 and B1, 2; these cladograms are essentially similar, except that the distribution of characters 1 and 3 are accounted for by convergence in cladograms A1, 2 and by reversal in B1, 2) and the resulting strict consensus cladogram are shown. In cladogram A1, taxa **a** and **c** are grouped by a synapomorphy for character 3, while in cladogram A2, **a** and **b** are grouped by a synapomorphy for character 1. When a strict consensus cladogram of A1 and A2 (also B1, B2) is produced, these three taxa are placed in a polytomy, and there is one extra step involved (five in cladograms C and D vs. four in A1, 2 and B1, 2) because reversals (C) or convergences (D) in characters 1 and 3 occur simultaneously. Miyamoto rejected the use of consensus cladograms in describing the distribution of character states and in the construction of classification. Anderberg and Tehler (1990: 401) agree with Miyamoto (1985) in suggesting that a resulting consensus cladogram will be similar to a cladogram that is less parsimonious than any of the minimal length cladograms produced from the original data set (for the reasons just discussed). These authors also agree with Miyamoto in noting that cladograms and consensus cladograms are based on different sources of information; a consensus cladogram is a summary of the **topologies** of all equally minimal length cladograms (i.e., the distribution of taxa in each of these cladograms), and **not** a summary of the distribution of the characters or character states that produced these topologies. Therefore, the distribution of character states should be considered apart from a resulting consensus cladogram. As a summary of topologies of all minimal length cladograms, Anderberg and Tehler (1990) support the use of consensus cladograms as a basis for constructing a classification, and this method will be followed in this analysis, as described earlier. As well, character distributions will not be read from the semistrict consensus cladogram shown in **Figure 26** for the reasons given by both Miyamoto (1985) and Anderberg and Tehler (1990), that cladograms and consensus cladograms are based on different sources of information, the original data set (including characters and character states), and the multiple minimal length cladograms produced, respectively.

The task becomes one of choosing which of the 36 minimal length cladograms used in constructing the semistrict consensus cladogram of **Figure 26** should be chosen for reconstucting the distribution of the character states. Since not all character distributions can be read directly from the consensus cladogram, the minimal length cladogram chosen should have a topology that is similar to that of the consensus cladogram (in terms of the taxa the researcher feels are most relevant; here taxa previously referred to *Alphadon*), since this latter cladogram is a summary of all equally well supported topologies, and is the one used in classification. It seems inappropriate to choose a minimal length cladogram to represent the character distributions in which monophyletic taxa are supported at certain nodes by synapomorphies if these same taxa are resolved as a polytomy in the consensus cladogram used in the final classification. The character distribution would then not be consistent with the classification. An example is the position of *A. halleyi* in certain of the 36 cladograms (**Appendix 3**) used to produce the semistrict consensus cladogram in **Figure 26**. In some of these, *A. halleyi* falls outside (and is sister taxon to) a larger group including *A. marshi*, *A. jasoni*, and *Turgidodon* (cladograms 23, and 24), while in others *A. halleyi* is the sister group to *Turgidodon* alone (cladograms 9, 10, 32, 33, 34, 35, 36). These sister group relationships, though supported by the character data on certain of the minimal length cladograms, would not be supported in the final classification.

In the semistrict consensus cladogram in **Figure 26**, the relationships of *A. halleyi*, *A. marshi* and *A. jasoni*, *Turgidodon* and the more derived ingroup marsupial taxa are resolved as a polytomy. The *Alphadon creber-Alphadon* sp., cf. *A. creber* and *Protalphadon lulli-Protalphadon* n. sp. A clades are successively more inclusive sister taxa to this polytomy, respectively. *Protalphadon* n. sp. B is the sister taxon to all these. All original cladograms are similar in preserving the positions of these latter three clades, and a large portion of these cladograms resolve the *Protalphadon lulli-Protalphadon* n. sp. A (26/36) clade as sister group taxa, as does the semistrict consensus cladogram. The resolution of *Turgidodon* as a monophyletic group is also seen in all original cladograms. The semistrict cladogram also resolves *A. marshi-A. jasoni* as sister taxa in a monophyletic clade, as do 18/36 of the original cladograms. One other element of the semistrict consensus cladogram is that *Alphadon halleyi* is not more closely related to either *Turgidodon*, or the *A. marshi-A. jasoni* clade. This element is preserved in original cladograms 6, 22 and 26. Of these three, the sister group relationship of *Protalphadon lulli-Protalphadon* n. sp. A is seen in original cladograms 22 and 26. Original cladogram 26 also resolves *Alphadon creber* and *Alphadon* sp., cf. *A. creber* as sister group taxa, which is not seen in the semistrict consensus tree in **Figure 26**. The only difference between the cladogram number 22 and the consensus cladogram in **Figure 26** is that in the former, the clade containing the more derived marsupial taxa is not part of the large polytomy, but is the sister group (positioned at the next most inclusive node) to it. This suggests that the more derived marsupial clade branched off before the *Turgidodon*, *A. halleyi* and *A. marshi-A. jasoni* polytomy, and that this polytomy possesses synapomorphies that the more derived marsupial clade lacks. However, when the character distributions on original cladogram 22 are examined, it is the more derived marsupial clade that possesses the majority of the synapomorphies, while the *Turgidodon*, *A. halleyi* and *A. marshi-A. jasoni* polytomy possesses the same state as the taxa at the less inclusive nodes. The exception to this is character **8**, the position of stylar cusp C relative to the edge of the stylar shelf. Members of the *Turgidodon*, *A. halleyi* and *A. marshi-A. jasoni* polytomy possess upper molars on which cusp C is more lingually placed, while all other taxa (including the more derived marsupial taxa) possess upper molars on which cusp C is more labially placed along the edge of the stylar shelf. Given all of these considerations, original cladogram 22 (**Figure 29**) is the most appropriate for examining the distributions of character states; the topology of this cladogram is generally similar to that of the semistrict consensus cladogram used in classification, except for the position of the more derived marsupial clade.

The character distributions that are of the greatest interest are, of course, the synapomorphies which define monophyletic taxa. These synapomorphies are mapped onto original cladogram 22 in **Figure 30**, and described below, beginning with the node where the outgroup taxa join the cladogram, and then proceeding through the less inclusive nodes. The outgroup taxa have been separated from *Alphadon* s.l. and the other included marsupial taxa on a separate branch. Deltatheroida is the most closely related of these outgroup taxa to *Alphadon* s.l. and the other marsupial taxa, but some character states that were originally suggested to be synapomorphies for a Deltatheroida-Marsupialia taxon (character **41**, numbers of premolars (state 2); character **43**, numbers of molars (state 1), Kielan-Jaworowska and Nessov, 1990), have been resolved on original cladogram 22 as plesiomorphies (or the same state as that assigned to the node at which the two major branches of the cladogram join), with the states in other outgroup taxa being resolved as synapomorphies. This is due to the fact that the PAUP 3.0 program will root the cladogram so that the designated ingroup (which did not include the Deltatheroida) is monophyletic, if possible. All ingroup taxa (those previously referred to *Alphadon* s.l., as well as *Protalphadon* n. sp. B and the members of the cohorts Ameridelphia and Australidelphia) share certain synapomorphies, including: characters **2**, position of stylar cusp A relative to cusp B (0-1 (A basal to B; reversal from 1-0 in more derived marsupial clade)); **19**, degree of separation of paracone and metacone at their bases (0 (connate)-1 (not connate)); and **25**, strength, morphology of the internal cristae (0 (absent (outgroup taxa, except *Kennalestes* (state 2))-1 (present, but weak and low)).

Protalphadon n. sp. B is the sister taxon to all other marsupial taxa, and is separated from these by characters **6**, morphology of stylar cusp C (0 (absent, *Protalphadon* n. sp. B)-1-2-3); **22**, labial extent of the bases of the paracone and metacone (0 (*Protalphadon* n. sp. B)-1); **37**, positions of the entoconid and hypoconulid relative to the hypoconid (0-1 ("twinned")); and **39**, position of the cristid obliqua at the posterior wall of the trigonid (0 (lingual to postcristid notch)-1 (basal to postcristid notch)). Characters from the lower molars were not coded for *Protalphadon* n. sp. B in this analysis, as discussed in Chapter 3. Lower molars referred to this genus by Cifelli (1990a; the original reference was to *Iqualadelphis lactea*) were considered to be incorrectly asscoiated with the upper molars referred in Chapter 3 to *Protalphadon* n. sp. B. This results in *Protalphadon* n. sp. B not possessing the character often considered to be a synapomorphy for the Marsupialia, "twinned" hypoconulid and entoconid. It must be recognized that the absence of this synapomorphy is based on a lack of evidence. Since *Protalphadon* n. sp. B is separated from other taxa referred to *Protalphadon*, it will have to be classified separately, in a new genus and species. This will be discussed in further detail in Chapter 5.

The Genus *Protalphadon* is restricted to *Protalphadon lulli* and *Protalphadon* n. sp. A, which are resolved in the semistrict consensus cladogram and in original cladogram 22 as a monophyletic group. Three characters support this group as a clade: **7**, the position of stylar cusp C relative to the ectoflexus (0-1 (*Protalphadon lulli* and *Protalphadon* n. sp. A); state 1 (cusp C anterior to ectoflexus) in *Turgidodon rhaister* and *Alphadon jasoni* are convergences) and **32**, development of the postmetacingulum (0-1 (*Protalphadon lulli* and *Protalphadon* n. sp. A); possession of state 1 (absence) in the more derived marsupial clade (Ameridelphia and Australidelphia) and in all outgroup taxa except *Prokennalestes*, are convergences), **24**, conule size (0 (smaller and weakly developed)-1 (larger and more strongly developed); possession of state 1 in the *A. halleyi*, *A. marshi - A. jasoni*, *Turgidodon* and the more derived ingroup marsupial clade is due to convergence). *Protalphadon* n. sp. A possesses two autapomorphic states within *Protalphadon*: **21**, the shape of the labial faces of the paracone and metacone (0-1 (*Protalphadon* n. sp. A); the possession of state 1 (concave labial faces) in *Alphadon jasoni* and *Peratherium* and *Ankotarinja* are convergences); and **23**, morphology of the centrocrista (0-2 (*Protalphadon* n. sp. A)).

Alphadon creber and *Alphadon* sp., cf. *A. creber* occupy the next most inclusive node, but are resolved as a polytomy; there is no uniquely derived character state which suggests that these two are a monophyletic group, but there are synapomorphies that separate these species from *Protalphadon*. This is contrary to the classification of Cifelli (1990a), and will be discussed in Chapter 5. As well, these taxa are separated from others previously assigned to *Alphadon*, and cannot retain this generic name. The synapomorphies which separate *Alphadon creber* and *Alphadon* sp., cf. *A. creber* from *Protalphadon* and group these former taxa with the *A. halleyi*, *A. marshi-A. jasoni*, *Turgidodon* and the more derived ingroup marsupial clade include: **16**, relative heights of the paracone and metacone (0 (paracone taller)-1 (subequal)); **17**, paracone and metacone relative sizes (widths) in labial view (0 (equal widths)-1 (metacone wider)); **18**, paracone and metacone shape and absolute sizes (0 (cusps sharp and uninlated)-1 (cusps rounder and conical). Certain characters are resolved as autapomorphies for *Alphadon* sp., cf. *A. creber* (discussed in Chapter 3), including characters **13**, anterior width of stylar shelf relative to posterior width on M3 (0 (anterior shelf as wide as the posterior shelf)-1 (narrower than the posterior shelf; *Alphadon* sp., cf. *A. creber*, the possession of state 1 in *A. halleyi* and *Peratherium* is convergent)); **14**, orientation of the postmetacrista (0 (oriented labially)-1 (oriented more posterolabially; *Alphadon* sp., cf. *A. creber*, possession of state 1 in *Peratherium* and *Ankotarinja*, Deltatheroida, and *A. halleyi* are convergences)); **15**, upper molar trends in size and shape of ectoflexus (1 (shallower on the anterior molars and increasing in depth posteriorly)-0 (deeper on all upper molars; *Alphadon* sp., cf. *A. creber*, state 0 in *A. halleyi*, Deltatheroida and *Turgidodon lillegraveni* are convergences)).

Other characters separate *Alphadon creber* and *Alphadon* sp., cf. *A. creber* from the *A. halleyi*, *A. marshi-A. jasoni*, *Turgidodon*, more derived ingroup marsupial clade, including: characters **6**, morphology of stylar cusp C stylar cusp C (1(variably present)-2 (consistently present)); **20**, relative separation of the paracone and metacone (0 (more closely approximated on the molar surface, *Alphadon creber - Alphadon* sp., cf. *A. creber*)-1 (more widely separate); **24**, conule size (0 (smaller and weakly developed, *Alphadon creber-Alphadon* sp., cf. *A. creber*)-1 (larger and more strongly developed); possession of state 1 in *Protalphadon* is due to convergence), **25**, strength, morphology of the internal cristae (1 (weak and low (*Alphadon creber-Alphadon* sp., cf. *A. creber*)-2 (more strongly developed); **26**, protocone length anteroposteriorly (0 (shorter anteroposteriorly, protocone compressed (*Alphadon creber-Alphadon* sp., cf. *A. creber*))-1 (anteroposteriorly longer); and **34** relative heights of the talonid and trigonid (from Cifelli, 1990a), 0 (talonid can be lower than the trigonid, *Alphadon creber-Alphadon* sp., cf. *A. creber*)-1 (talonid can be closer to the trigonid in height).

At the next most inclusive node are the taxa that were included as the more derived marsupial taxa, including representatives of the cohorts Ameridelphia (*Peratherium*) and Australidelphia (*Ankotarinja* and *Andinodelphys*). This clade is resolved on the original cladogram number 22 as the sister group to the polytomy including *A. halleyi*, *A. marshi - A. jasoni*, and *Turgidodon*. As discussed earlier, this resolution is supported by only one character, while the monophyly of the of the more derived marsupial clade is supported by several synapomorphies. In these instances, the *A. halleyi*, *A. marshi-A. jasoni*, and *Turgidodon* polytomy shares the same state with taxa (*Protalphadon*, *Alphadon creber - Alphadon* sp., cf. *A. creber*) at more inclusive nodes. These relationships will be discussed further below, and in Chapter 5. The synapomorphies supporting the resolution of the more derived marsupial taxa (cohorts Ameridelphia and Australidelphia) as a monophyletic group separate from taxa previously referred to *Alphadon* s.l. are the following: characters **1**, size of stylar cusp A (1 (larger)-0 (smaller), reversal); **2**, position of cusp A relative to B (1 (basal to cusp B)-0 (more closely approximated at the level of the stylar shelf), reversal); **15**, shape of ectoflexus on M1-3 (1-2 (shallow on M1- 3)); **16**, relative heights of the paracone and metacone (1 (subequal)-2 (paracone shorter than metacone)); **18**, shape and absolute size of paracone and metacone (1 (rounder, conical)-0 (sharp and uninflated), reversal, with a second reversal from 0-1 in *Peratherium* and *Ankotarinja*); **28**, position of the protocone relative to the paracone (0 (protocone posterior to paracone)-1 (protocone more in line with paracone), with reversal from 1-0 in *Peradectes*; possession of state 1 in *Kennalestes -Prokennalestes* is convergent); **32**, presence or absence of the postmetacingulum (0 (present)-1 (reduced to absent; possession of state 1 in the outgroup taxa (except *Prokennalestes*), and *Protalphadon* is convergent)); **35** shape of the entoconid (0-1 (narrower), and 1-2 ("spire-like" (Crochet, 1979, 1980) in *Peratherium* and *Ankotarinja*); **39** position of the cristid obliqua at the posterior wall of the trigonid (1-2 (labial to protocristid notch)). Other character states are synapomorphies for taxa within this larger clade. The characters include: **3**, size of stylar cusp B (0 (largest stylar cusp on the stylar shelf)-2 (smaller and more equal in size to cusps C and D; grouping *Peradectes, Peratherium* and *Ankotarinja*)); **14**, orientation of the postmetacrista (0 (oriented labially)-1 (oriented more posterolabially; grouping *Peratherium* and *Ankotarinja*, possession of state 1 in Deltatheroida, *Alphadon* cf. *A creber* and *A. halleyi* are convergences)); **21**, the shape of the labial faces of the paracone and metacone (0-1 (*Peratherium* and *Ankotarinja*); the possession of state 1 (concave labial faces) in *Alphadon jasoni* and *Protalphadon* n. sp. A are convergences); **23**, morphology of the centrocrista (0-3 (*Peratherium* and *Ankotarinja*; the possession of state 3 (the apex of centrocrista U-shaped, reaching the level of the stylar cusps (dilambdodont) in *Alphadon jasoni* is due to convergence)); **30**, depth of the trigon basin (0 (deep)-1 (shallow; *Peratherium* and *Ankotarinja*; the possession of state 1 in *Turgidodon* (except for *T. madseni*) is convergent); **38**, position of the hypoconulid relative to the entoconid (0 (hypoconulid more labioposteriorly positioned relative to the entoconid)-1 (hypoconulid more posteriorly positioned so that the hypoconulid is more directly posterior to the entoconid; *Peratherium* and *Ankotarinja*).

The next most inclusive node on original cladogram 22 involves the major polytomy including *Alphadon halleyi, A. marshi--A. jasoni* and *Turgidodon. Turgidodon* and *A. marshi -A. jasoni* are both resolved as monophyletic groups, but the position of *A. halleyi* is ambiguous. This clade is separated from that just described above (including *Peradectes, Peratherium, Ankotarinja* and *Andinodelphys*) by one character, character **8**, position of stylar cusp C relative to the labial edge of the stylar shelf (0 (cusp C placed along the labial edge of the stylar shelf)-1 (cusp C more lingually placed; *Alphadon halleyi, A. marshi - A. jasoni* and *Turgidodon*, and 1-2 (extremely lingually placed, closer to the labial base of the paracone) in *T. rhaister*, with reversal (1-0) in *T. madseni*). This is the only character supporting the polytomy including *Alphadon halleyi, A. marshi -A. jasoni* and *Turgidodon*, while several other characters (described above) group this polytomy with the more derived marsupial clade, and separate these from other taxa previously referred to *Alphadon* s.l. (i.e., *Alphadon creber -Alphadon* sp., cf. *A. creber, Protalphadon*).

Within the polytomy including *Alphadon halleyi, A. marshi -A. jasoni* and *Turgidodon, A. marshi* and *A. jasoni* are grouped as a clade on the basis of only one character (**Figure 30B**), character **23**, shape and general morphology of the centrocrista (0 (centrocrista straight (predilambdodont or rectidont))-1 (centrocrista V-shaped, with the apex reaching the lingual side of stylar cusp C, and the valley between the paracone and metacone broad and shallow; *A. marshi*) and 1-3 (centrocrista apex U-shaped and reaching the level of the stylar cusps; *A. jasoni*, the presence of state 3 as a synapomorphy grouping *Peratherium* and *Ankotarinja* is convergent). On the strict consensus cladogram produced from the ordered and reweighted data, *A. marshi* and *A. jasoni* were not resolved as a monophyletic subgroup, and it is apparent that the only character evidence grouping these two and separating them from *A. halleyi* involves changes in the morphology of the centrocrista, such that the transformation series for these states involves a change from state 0 (centrocrista straight; outgroup taxa, *Protalphadon* n. sp. B, *Protalphadon* (except *Protalphadon* n. sp. A), *A. creber*, *Alphadon* sp., cf. *A. creber*) to state 1 (centrocrista V-shaped, with the apex reaching the lingual side of stylar cusp C, and the valley between the paracone and metacone broad and shallow; state at node joining *A. marshi* and *A. jasoni*, and retained in *A. marshi*) to state 3 (centrocrista U-shaped, apex reaching row of stylar cusps). In Chapter 2 it was stated that the distribution of character states on the cladogram would be used as evidence for reconstructing transformation series in the absence of any *a priori* evidence. However, *A. marshi* and *A. jasoni* were resolved as a monophyletic group on the semistrict consensus cladogram (**Figure 26**) because of the presence of state 0 for character **23** in most of closely related taxa at less inclusive nodes as well as *A. halleyi* and *Turgidodon*, and because this clade (characterized by V-shaped centrocrista, *A. marshi* (state 1) and *A. jasoni* (state 3)) did not conflict with any component or clade on the strict consensus cladogram. The resolution of taxa on the strict consensus cladogram (and the use of an original cladogram reflecting this resolution to examine the character distribution) would suggest that states 1 and 3 for *A. marshi* and *A. jasoni* would have arisen convergently from state 0. Since other character evidence suggesting that *A. marshi* and *A. jasoni* are a monophyletic group is lacking (compared to *Protalphadon*, also resolved as a clade on the semstrict but not strict consensus tree), and because of the other morphological differences between the morphologies of the centrocrista of *A. marshi* and *A. jasoni* (as discussed in Chapter 3), and the unnecessary confusion in classification that would result if *A. halleyi* were separated from *A. marshi* and *A. jasoni* (*Alphadon* would have to be restricted to these latter two taxa, *A. halleyi* would have to be assigned to a new genus), *A. marshi* and *A. jasoni* are included in the larger polytomy with *A. halleyi* and *Turgidodon*, as discussed further in the final classification presented in Chapter 5. Several character states are resolved as autapomorphies for *Alphadon jasoni*, including character **23**, just described, also character **7**, position of cusp C relative to the ectoflexus (0 (cusp C positioned at the deepest part of the ectoflexus)-1 (cusp C positioned anterior to the deepest part of the ectoflexus; convergent in *Protalphadon* and *Turgidodon rhaister*) and **21**, the shape of the labial faces of the paracone and metacone (0-1 (*A. jasoni*); convergences as described above).

Within the polytomy, several character states are resolved as autapomorphies for *A. halleyi*, including those associated with characters **9**, orientation of stylar cusp C relative to the edge of the stylar shelf (0 (stylar cusp C oriented anteroposteriorly)-1 (oriented anterolingually-posterolabially; state 1 grouping *T. praesagus* and *T. russelli* is considered convergent); **13**, anterior width relative to posterior width on penultimate upper molar (0 (anterior shelf as wide as the posterior shelf)-1 (anterior shelf narrower than the posterior shelf; *A. halleyi*; convergences as discussed earlier); **14**, orientation of the postmetacrista (0 (oriented labially)-1 (oriented more posterolabially; *A. halleyi* , convergencces as discussed earlier); **15**, upper molar trends in size and shape of ectoflexus (1 (shallower on the anterior molars and increasing in depth posteriorly)-0 (deeper on all upper molars; *Alphadon* sp., cf. *A. creber*, state 0 in *A. halleyi*, Deltatheroida and *Turgidodon lillegraveni* are convergences)); **29**, presence or absence of protoconal cingula or rugosities (0 (protoconal cingula or rugosities entirely absent)-1 (protoconal cingula or rugosities on the posterior side of the protocone, or on both the anterior and posterior sides of the protocone; *A. halleyi*, presence of protoconal cingula in all species assigned to *Turgidodon* (except *T. madseni*) and in *Kennalestes* are convergences).

Synapomorphies grouping species of *Turgidodon* as a monophyletic group are associated with characters **4**, height of B relative to the paracone and the protocone (0 (cusp B can be shorter or smaller than the paracone and the protocone)-1 (cusp B more nearly equal in height to the paracone and the protocone); **25**, strength, morphology of the internal cristae (2 (internal cristae more strongly developed) - 3 (internal cristae high, wall-like structures that are less crest-like; *Turgidodon*); **42**, general morphology of the premolars (0 (less robust and bulbous)-1 (more robust and bulbous; *Turgidodon*). The taxon at the basal node for *Turgidodon*, *T. madseni* was originally assigned to *Turgidodon* by Cifelli (1990a: 306) but described as being more gracile and less bulbous. This taxon does not share several of the synapomorphies discussed below, and therefore, there are not as many synapomorphies supporting *Turgidodon*, but several that support various nodes within *Turgidodon*. In the classification presented in Chapter 5, the phyletic sequencing method is used to portray the sister group relationships of these taxa to one another, without the need for naming higher-level taxa at each new node within *Turgidodon*.

Characters grouping various species within *Turgidodon* include characters **3**, size of stylar cusp B (0 (stylar cusp B is the largest stylar cusp on the stylar shelf)-1 (stylar cusp B is hypertrophied, with labial expansion; a synapomorphy for all taxa assigned to *Turgidodon* except *T. madseni*); **5**, strength of crests contributing to the preparacrista from the paracone and stylar cusp B (0 (crests from the paracone and stylar cusp B equal in strength so that the crest from cusp B is easily seen in occlusal view and extends to the apex of cusp B)-1 (crest from cusp B weak and more difficult to see in occlusal view; a synapomorphy grouping all taxa assigned to *Turgiodon* except *T. madseni*); **9**, orientation of stylar cusp C relative to the edge of the stylar shelf (0 (stylar cusp C oriented antero-posteriorly)-1 (oriented anterolingually-posterolabially; synapomorphy grouping *T. praesagus* and *T. russelli*; convergences as described above); **10**, size of C relative to D on penultimate molar (0 (cusp C smaller than D on penultimate molar)-1 (cusp C larger than D; convergent within *Turgidodon* for *T. madseni* and *T. russelli*); **11**, cusp C shape in labial view (0 (cusp C conical)-1 (squared at its apex; this state groups *T. rhaister*, *T. praesagus* and *T. russelli* as a clade); **17**, relative sizes of the paracone and metacone in labial view (1 (metacone larger (broader anteroposteriorly) than the paracone)-2 (paracone larger than the metacone; autapomorphy for *T. lillegraveni*); **27**, basal posterior expansion of the protocone (0 (basal posterior portion of the protocone may be unexpanded)-1 (basal posterior portion of the protocone expanded so that this part of the protocone is lobe-like; a synapomorphy for *T. rhaister*, *T. praesagus* and *T. russelli*); **29**, presence or absence of protoconal cingula or rugosities (0 (protoconal cingula or rugosities entirely absent)-1 (protoconal cingula or rugosities on the posterior side of the protocone, or on both the anterior and posterior sides of the protocone; synapomorphy grouping all species assigned to *Turgidodon* except *T. madseni*, convergences as discussed above); **30**, depth of the trigon basin (0 (deep)-1 (shallow; a synapomorphy grouping all species assigned to *Turgidodon* (except for *T. madseni*), convergences as discussed above).

The character distributions at each node on original cladogram 22 have been described. Each node is supported by a certain number of synapomorphies (**Figure 30**), except for the node expressing the polytomy including *Alphadon halleyi*, *A. marshi* -*A. jasoni* and *Turgidodon*, which is only supported by character **8**. Character states possessed by taxa within this polytomy were described above as autapomorphies, and in several instances, taxa outside the polytomy possessed similar states. These similarities were resolved as convergences. The final classification of these taxa is presented in Chapter 5. This classification is based on the semistrict cladogram in **Figure 26**, but with *Alphadon* *jasoni* and *A. marshi* resolved, not as a monophyletic clade as suggested by this cladogram, but as unresolved parts of the polytomy, similar to *A. halleyi*.

CHAPTER 5

CLASSIFICATION

The distribution of species previously assigned to *Alphadon* s.l. can be read from the topology of the semistrict consensus cladogram in **Figure 26**. The classification presented in this chapter is derived from **Figure 26**, with modifications regarding to *A. marshi* and *A. jasoni* as noted at the end of the last chapter. The reasons for basing the classification of *Alphadon* s.l. on this consensus cladogram were adequately treated in Chapter 4.

The correspondence between a cladogram and the resulting Linnaean classification was discussed in depth by Eldredge and Cracraft (1980). As these authors note, the structure of the classification follows from the structure of the relationships of the taxa being classified. If the structure of these relationships is expressed in a cladogram, then the classification of these taxa follows directly from the topology of the cladogram. Eldredge and Cracraft (1980: 168, 170-1) stress that there must be a one-to-one correspondence between this cladogram and the classification, such that the hierarchy of taxa in the cladogram (or the nested sets of taxa) represents the information content of the classification (and the information retrievable from the classification). The classification presented in this chapter follows directly from the topology of the consensus tree or cladogram as much as possible, but necessarily diverges from this one-to-one classification when dealing with the classification of the taxa included in the major polytomy in **Figure 26**.

There are certain problems involved in strictly deriving a classification from a cladogram. For example, Tassy (1989) has suggested that several equally valid "cladistic" classifications can be obtained from a single cladogram. Ramsköld and Werdlin (1991) have also noted that arbitrary decisions (i.e., in determining ranks of taxa) must be made in translating a cladogram into a classification, and because of this, and because all relevant information is provided in the structure of the cladogram (also Gauthier et al., 1988a), they do not provide a classification in their analysis.

As well, as originally suggested by Hennig (1966), sister taxa on the cladogram should be given equal categorical ranks in the classification. This results in a large number of higher categorical ranks in the classification; for example, the classification of the Class Mammalia presented by McKenna (1975) illustrates this problem. Secondly, if a node on the cladogram is represented by a single species (i.e., *Protalphadon* n. sp. B), it would still have to classified at a rank equal to that of its sister taxon (in **Figure 26**, all nodes above *Protalphadon* n. sp. B). If the rank for the larger sister group was, for example, Cohort, then *Protalphadon* n. sp. B would be ranked at the cohort level, but would also require Order, Family, Subfamily, etc. rankings, resulting in a series of extraneous monotypic taxa, so called because *Protalphadon* n. sp. B would be the only species classified in these higher categories.

Various conventions have been derived to overcome the problem of the proliferation of categorical ranks, including monotypic (redundant) ranks; these methods follow from two features inherent in the Linnaean classification- the indenting or subordination of taxa of unequal rank and the listing of taxa of equal rank. Phyletic sequencing (Nelson, 1972, 1973; Cracraft, 1974; Eldredge and Cracraft, 1980: 226-9; Wiley, 1981) uses the second property of the Linnaean classification, and involves a listing of taxa in a classification to express relationship, reflecting the branching sequence on the cladogram (Nelson, 1972; 229; 1973) such that each taxon in the sequence is the sister taxon of all taxa below it in the sequence. Here, the relationships of the taxa to one another are described within the classification, but without the need for higher taxonomic ranks at each branch. Phyletic sequencing was originally described as involving taxa of **equal** rank. By this method, *Protalphadon* n. sp. B, ranked at the subfamily or family level, would be the first taxon listed in the sequence, and as such would be the sister taxon to all taxa (of equal rank) below it. Unfortunately, since *Protalphadon* n. sp. B is a single species ranked at higher taxonomic levels (subfamily or family level), these would be monotypic taxa. However, Eldredge and Cracraft (1980: 227) suggest that rank is not important in the phyletic sequencing method, since it does not affect the information content of the classification (sister group relationships).

The phyletic sequencing method is applicable to only certain types of branching diagrams: "dichotomous" (Nelson, 1973) or "asymmetrical" (Wiley, 1981: 209). The cladogram used for the classification in this analysis contains a major polytomy, and is only fully resolved near its base. Nelson (1973: 348) describes this type of branching diagram as "aspect BB", in comparison to a fully resolved dichotomous branching diagram ("aspect B"), and suggests that while the sequencing methodology can be used to classify the taxa in this former diagram, it is not generally applicable to the "aspect BB" diagram. This suggests that the phyletic sequencing method may not be as useful in producing a classification from **Figure 26**. As Wiley (1981: 210) notes, the sequencing methodology cannot be used when polytomies are present unless there is some method for differentiating between a (sequenced) list of taxa describing dichotomies and sister group relationships, and a list of taxa describing taxa of uncertain relationship in the polytomy. Wiley (1981: 211) suggests that in a classification, polytomous taxa be given equal rank and designated "*sedis mutabilis*". By the use of this convention, the sequencing method can be retained to indicate sister group relationship.

As well, Wiley (1981: 203) described a system called "subordination by pure indentation", which reflects the first property of the Linnaean classification noted above. By subordinating taxa in a classification, their hierarchical relationships are represented in an indented list; less inclusive or subordinate taxa are indented below the more inclusive taxa to which they belong, and sister taxa have the same degree of indentation. This method also avoids the problem of the creation of a large number of taxa at each node. Wiley (1981: 203-4) criticized indented classifications, because of difficulties involved in easily visualizing which groups in the indented list were sister taxa. Recently however, Gauthier et al. (1988a, b) have utilized indented classifications in their discussions of the Lepiodosauromorpha (Gauthier et al., 1988a) and the Amniota (Gauthier et al., 1988b). For these taxa, Gauthier et al. (1988a, b) represent relationships as a list in which less inclusive taxa are more indented in the classifications than the more inclusive taxa. Gauthier et al. (1988a) still use more inclusive taxonomic names to incorporate less inclusive taxa, for example, the first branch of their final cladogram (Gauthier et al., 1988: fig. 3) is represented by the higher-level taxonomic name "Mammalia", while the second branch is represented by "Reptilia", but they reject the use of categorical rank altogether. Gauthier et al. (1988a: 60) do not use the phyletic sequencing method because although this method does not create large numbers of categorical names, as a list of taxa representing sister group relationships, it leaves several taxa unnamed, that is, the more inclusive taxa, like "Reptilia", under which several less inclusive taxa would be subordinated in the classification. Polytomous taxa are represented by equal indentation (Gauthier et al., 1988a: 63), rather than by the use of terms like "*sedis mutabilis*".

The final classification for this analysis is presented below, and focuses on species previously referred to *Alphadon* s.l. (and species assigned to *Protalphadon* and *Turgidodon* by Cifelli, 1990a). The methodology used to produce this classification follows, for the most part, the suggestions of Gauthier et al. (1988a,b) in the use of the "subordination by indentation" methodology, and in the absence of categorical rank. However, the phyletic sequencing method is used for classifying the lower nodes of the second branch in **Figure 26** because this part of the cladogram is fully resolved, and the relationships of the taxa can then be expressed without having to classify these taxa together at a higher level (for example, with regards to *Protalphadon* n. sp. B). The phyletic sequencing convention is also used for *Turgidodon*, which again avoids the need for additional higher-level taxa at each fully resolved node. The use of equal indentation to represent polytomous taxa (as suggested by Gauthier et al., 1988a) and the phyletic sequencing method to represent sister group relationships in this classificaton are, however, incompatible (i.e., Wiley, 1981). For example, using phyletic sequencing, the classification of the taxa at the first three fully resolved nodes on the second major branch of the cladogram in **Figure 26** would be as follows-

- *Protalphadon* n. sp. B
- *Protalphadon*
  - *Protalphadon lulli*
  - *Protalphadon* n. sp. A
- new genus B
  - *"Alphadon" creber*
  - *"Alphadon"* sp., cf. *"A." creber*

Given only this classification, and the stated use of both methods described above, it is not clear whether *Protalphadon* n. sp. B, *Protalphadon*, and the new genus B are sister groups, as indicated by the sequencing convention, or polytomous taxa, as indicated by the use of equal indentation. To overcome this problem, Wiley's "*sedis mutibilis*" could be used, or alternatively, the metataxon (Gauthier et al., 1988a; = metaspecies, Donoghue, 1985) designation could indicate when taxa are resolved as a polytomy. Metataxa are groups for which there is no character evidence for either monophyly or non-monophyly, that is, the taxa are resolved as polytomies. As such, they are given the "benefit of the doubt", until new evidence is found to either support monophyly, or to reject it (Donoghue, 1985: 178). Metataxa are represented in classification by an asterisk at the end of the metataxon name (Gauthier et al., 1988a: 16). Gauthier et al. (1988a) note that the metataxon convention be used only for taxa whose names are already established, and should not be used to create new taxon names. This suggestion is followed as far as possible in the classification presented in this chapter; however, a new taxon ,"new genus B*", is named to include species previously referred to "*Alphadon creber*", which were resolved in **Figure 26** as a dichotomy. This is simply to reduce the number of additional conventions used in this classification (i.e., "*sedis mutibilis*").

As well, the use of the metataxon has been recently criticized by Kluge (1989: 292), who suggested that a polytomy (and the resulting metataxon) may be the result of character incongruence rather than the absence of character evidence. By character incongruence, Kluge refers to the consensus cladogram, which again, is a summary of the topologies of all minimal length trees, supporting only those components for which there is unequivocal character evidence (Anderberg and Tehler, 1990: 401). Because of this, consensus trees will be less well resolved than any of the minimal length trees, including taxa whose relationships are resolved as polytomies. Kluge argues that when classifications are derived from a consensus cladogram (as in this analysis), and a polytomy identified in the classification as metataxon, this metataxon designation is based on incongruent characters (i.e., in some of the minimal length trees, certain characters would have resolved the relationships of these taxa, but because these characters are incongruent in these minimal length trees, a polytomy results in the consensus cladogram, i.e., **Figure 28**), rather than the **absence** of character evidence. Incongruent characters, Kluge (ibid.: 292) argues, do not imply that these metataxa are "possibly" monophyletic, but rather, are paraphyletic. Kluge supports the use of Wiley's term "*sedis mutabilis*" for describing these polytomies in a classification. While Kluge has made a useful criticism, the consensus cladogram is a summary of the clades that are unequivocally supported by the character evidence at hand. If taxa are resolved as polytomies in this consensus cladogram, then the character support is not equivocal- there may be support for monophyletic clades in the various minimal length cladograms, but the composition of these clades varies from cladogram to cladogram, and there is no **unequivocal** evidence for monophyly or non-monophyly of the taxa involved (or which taxa are more closely related to taxa outside the polytomy). I believe that the metataxon designation can be applied to polytomies in the consensus classification, because as given in the original definition (Donoghue, 1985), there is no [unequivocal] character evidence suggesting whether or not the taxa in the polytomy are monophyletic or not.

Categorical ranks are not used in this classification. Gauthier et al. (1988a,b) rejected categorical ranks because the use of these has not been consistent between taxa that otherwise differ in taxonomic and morphological diversity (Gauthier et al., 1988a: 60). Beyond this, categorical ranks are unnecessary, since an indented classification adequately shows the relationship of taxa to one another, including taxa that are subordinated within others. In this classification, higher level, or more inclusive taxa and metataxa are used to include subordinate taxa and metataxa. In **Figure 26**, three species, *Alphadon halleyi*, *A.*

marshi and *A. jasoni* are part of the major polytomy including these taxa, *Turgidodon* and the more derived marsupial taxa. Both *Turgidodon* and the more derived marsupial taxa are monophyletic, but their relationships to *Alphadon halleyi*, *A. marshi* and *A. jasoni* are unresolved. These relationships of these taxa within the polytomy are best expressed through the use of higher level metataxa.

In the classification presented below, new taxonomic names (in bold) are applied that reflect the position of the taxon on the cladogram, that is, its relationship to other taxa. For example, the taxon previously referred to as *Protalphadon* n. sp. B is classified below as **new genus A, new species A**, which reflects the restriction of the name *Protalphadon* to the two taxa at the next less inclusive node, *P. lulli* and *Protalphadon* n. sp. A. *Alphadon creber* and *Alphadon* sp., cf. *A. creber* are assigned to a new, unnamed genus (**new genus B***), since these two species are not included in the major polytomy along with *Alphadon halleyi*, *A. marshi* and *A. jasoni*, and they are separated from *Protalphadon* (contrary to Cifelli, 1990a). These changes are the result of differences in how these taxa were originally believed to be classified, to how they are finally classifed below after the phylogenetic analysis described in Chapter 4. These newly named taxa are represented in **Figure 31** (the semistrict cladogram used in **Figure 26**, with changes in the relationship of *A. marshi* and *A. jasoni*, as described in Chapter 4), which can be compared to this classification.

CLASSIFICATION OF TAXA PREVIOUSLY REFERRED TO *ALPHADON* S.L.

Marsupialia

- **new genus A, new species A**
- ***Protalphadon*** Cifelli, 1990a
    - *Protalphadon lulli*
    - *Protalphadon* n. sp. A
- **new genus B***
    - n. gen. B *creber**
    - n. gen. B, cf. n. gen. B *creber**

- **new taxon B**
    - **Alphadontinae*** Marshall et al. (1990)
        - ***Turgidodon*** Cifelli, 1990a
            - *Turgidodon madseni*
            - *Turgidodon lillegraveni*
            - *Turgidodon rhaister*
            - *Turgidodon praesagus*
            - *Turgidodon russelli*
            - *Turgidodon petiminus*

        - ***Alphadon* s.s.*** Simpson, 1927
            - *Alphadon* marshi*
            - *Alphadon* halleyi*
            - *Alphadon* jasoni*
            - *Alphadon** sp., cf. *A.* jasoni*

    - **Australidelphia** Szalay, 1982
    - **Ameridelphia** Szalay, 1982

The discussion of this classification will make reference to recent classifications of *Alphadon* s.l. by Marshall et al. (1990) and Cifelli (1990a).

NEW GENUS A, NEW SPECIES A. This species was originally described as *Iqualadelphis lactea*, but several differences between materials referred to this species by Cifelli (1990a) and materials referred by Fox (1987a, b) were discussed in Chapter 3. The specimens referred by Cifelli were removed from *I. lactea*, and though originally referred to as *Protalphadon* n. sp. B., are assigned here to a new unnamed genus and species (a formal classification for this new taxon was given in Chapter 3 under *Protalphadon* n. sp. B and will not be repeated here). **New genus A, new species A** is separated from species retained in *Protalphadon* by two characters, as discussed in Chapter 4, but maintains the same phylogenetic relationship to this taxon (and others previously assigned to *Alphadon* s.l.) originally suggested by Cifelli (1990a): plesiomorphic sister taxon to all other more derived marsupial taxa.

PROTALPHADON. *Protalphadon* was originally diagnosed by Cifelli (1990a) on the basis of the possession of plesiomorphic character states relative to the remaining taxa previously assigned to *Alphadon* s.l., and to the Marsupialia as a whole (also Marshall et al., 1990). Following Cifelli's classification, the three taxa included in *Protalphadon* (*P. lulli*, *P. creber* and *P. wahweapensis*) would be grouped as a basal trichotomy on a cladogram, so that no available characters suggest which two species are more closely related to one another relative to the third. Rather than describing *Protalphadon* as a paraphyletic taxon (on the basis of plesiomorphic character states, or as a taxon not including all descendants (i.e., *Alphadon* s.s. and *Turgidodon*) of the common ancestor), the term "metataxon" would be applied. As described above, a "metataxon" refers to a group in which the relationships of the included taxa are not resolved by any information from the available characters. If new characters are found which indicate that some taxa within the metataxon are more closely related to other derived groups, then the metataxon becomes "positively paraphyletic" (Donoghue, 1985: 178). This is the case with *Protalphadon*. The final cladogram produced in this analysis (**Figure 26**), suggests that "*A.*" *creber* s.s. and "*Alphadon*" sp., cf. "*A.*" *creber* be included in a metataxon that is more closely related to Cifelli's *Alphadon* s.s. (taxa previously referred to *Alphadon*, but not included in *Protalphadon* or *Turgidodon*), and *Turgidodon* than to *Protalphadon*. Therefore, contrary to the classification of Cifelli (1990a), *Alphadon creber* s.l. ("*A.*" *creber* s.s. and "*Alphadon*" sp., cf. "*A.*" *creber*) should be removed from *Protalphadon*, and assigned to a new genus (**new genus B***). This closer relationship is based on synapomorphies described in Chapter 4, and mapped on **Figure 30**. The clade which retains the name ***Protalphadon***, including *Protalphadon lulli* and *Protalphadon* n. sp. A, falls outside this larger group, because these taxa lack the synapomorphies grouping "*A.*" *creber* s.s. and "*Alphadon*" sp., cf. "*A.*" *creber* with taxa included in the larger polytomy. ***Protalphadon*** does not include *A. creber* s.l., *P. wahweapensis* or *P. crebreforme*. These latter two taxa are either synonymized with "*Alphadon*" sp., cf. "*A.*" *creber* (*P. wahweapensis*) or considered to be too poorly known to be included in this analysis (*P. crebreforme*). A revision of ***Protalphadon*** is given in which the paraphyly of this genus is resolved by removing the two taxa that resulted from the revision of *A. creber* s.l.

Synapomorphies supporting the resolution of *Protalphadon* n. sp. A and *P. lulli* as a monophyletic clade were discussed in Chapter 4.

PROTALPHADON Cifelli, 1990a.

Type species. *Protalphadon lulli* (Clemens, 1966).

Included species. The type and *Protalphadon* n. sp. A.

Distribution. Lance Formation, Wyoming; "Mesaverde" Formation, Wyoming; Hell Creek Formation, Montana; Judithian and Lancian NALMAs.

Revised Diagnosis. Separated from species referred to **new genus B***, ***Alphadon* s.s.*** and ***Turgidodon*** by- paracone taller than metacone, generally equal width in labial view; postcingulum absent; stylar cusp C, when present, anterior to ectoflexus; cusp D reduced, especially on M3; differs from **new genus B***- conules larger and more strongly developed; similar to **new genus B***, differs from ***Alphadon* s.s.*** and ***Turgidodon*** in- stylar cusp C variably present; paracone and metacone more closely approximated on the molar surface; protocone shorter anteroposteriorly, protocone compressed; talonid lower than the trigonid.

Description and Discussion. *Protalphadon* Cifelli, 1990a was originally erected to include *P. lulli*, *P. creber*, and the new species, *P. wahweapensis*. In a second paper, Cifelli (1990b) referred *P. crebreforme* (Wahweap Formation, Utah, Aquilan) to this genus. These species possessed characters similar to those in the ancestral marsupial morphotype, including overall molar size, a high upper molar width to length ratio, a closely appressed paracone and metacone and a compressed paracone. Marshall et al. (1990: 437) described other characters associated with the ancestral morphotype or the stem marsupial, including a wide stylar shelf, deep ectoflexus and a linear centrocrista. Species classified in *Protalphadon* were separated from others once referred to *Alphadon* s.l. by the possession of characters listed above, as well as the variable possession of stylar cusp C (Cifelli, 1990a). While this classification had some utility in that *Alphadon* and *Turgdidon* could be characterized by synapomorphic character states (Cifelli, 1990a), *Protalphadon* was a metataxon, in which the relationships of the included taxa were not resolved by the available character information. Evidence from other characters (i.e., relative heights and widths of the paracone and metacone in labial view) suggests that "*Alphadon*" *creber* s.s. and "*Alphadon*" sp., cf. "*A.*" *creber* are more closely related to other species previously referred to *Alphadon* s.l. than are taxa referred above to ***Protalphadon***. Upper molars referred to "*Alphadon*" *creber* s.s. and "*Alphadon*" sp., cf. "*A.*" *creber* show a subequal paracone and metacone, with the metacone being wider in labial view. These states are shared with the remainder of *Alphadon* s.l., but not with *Protalphadon*.

NEW GENUS B*

Type species. new genus B* sp., cf. new genus B* *creber* (this species will be given a formal name for publication).

Included species. The type and new genus B* *creber*.

Distribution. Milk River Formation, Alberta, Kaiparowits and Wahweap formations, Utah, Aquilan NALMA.

Diagnosis. Differs from ***Protalphadon*** in- paracone and metacone subequal in height; metacone wider than paracone in labial view; paracone and metacone rounder and conical; differs from polytomy including *A. halleyi*, *A. marshi*, *A. jasoni*, *Turgidodon* and the more derived ingroup marsupial clade in- stylar cusp C variably present; paracone and metacone more closely approximated on the molar surface, conules smaller and more weakly developed; internal conular cristae weak and low; protocone shorter anteroposteriorly, protocone compressed; talonid lower than the trigonid.

Discussion. **New genus B*** is a new genus erected to include "*Alphadon*" sp., cf. *A. creber* and "*Alphadon*" *creber* s.s., two species whose materials had previously been assigned to "*Alphadon creber*". Character evidence suggests that "*Alphadon*" sp., cf. *A. creber* and "*Alphadon*" *creber* s.s. are not referable to ***Protalphadon***, even though both taxa share the variable possession of stylar cusp C on the upper molars. However, since the variable presence of stylar cusp C is a state distinct from that in the outgroup taxa and **new genus A, new species A** (cusp C absent), and in more derived taxa (cusp C consistently present on referred upper molars), it could be said to characterize a more inclusive taxon including ***Protalphadon*** and **new genus B***. However, a higher-level taxon erected to include ***Protalphadon*** and **new genus B*** would be paraphyletic for the same reasons that *Protalphadon sensu* Cifelli is a paraphyletic taxon, because of the synapomorphies indicating that **new genus B*** is more closely related to the more derived taxa at nodes further up the cladogram. In other words, this higher level taxon would not include all descendants of the last common ancestor of the taxon (i.e., members of the major polytomy), and., therefore, is not included in the classification above.

TURGIDODON, ALPHADON* s.s*, NEW TAXON B and ALPHADONTINAE. Several synapomorphies (**Figure 30**) separate members of the **new genus B*** from the other taxa grouped at the next less inclusive node on the final cladogram. To reflect this, these latter taxa are classified in **new taxon B**. The relationships of the taxa assigned to **new taxon B** to one another are not well resolved. There are two monophyletic groups, supported by several synapomorphies (**Figure 30**)- ***Turgidodon*** and the clade including *Peradectes* and members of the Ameridelphia and Alphadelphia. The relationships of the remaining species previously assigned to *Alphadon* s.l. are not well resolved. As discussed in Chapter 4, though *Alphadon marshi* and *A. jasoni* are resolved as a monophyletic clade in **Figure 26**, they are not retained as such, and are included individually in the polytomy, as is *Alphadon halleyi*. This resolution of these taxa is similar to that in strict consensus cladogram produced (**Figure 25**). *Alphadon marshi*, *A. jasoni* and *Alphadon halleyi* are retained in the genus ***Alphadon* s.s.***, which, to reflect the relationships of the assigned taxa to one another, is now designated as a metataxon. The relationship of ***Alphadon* s.s.*** to ***Turgidodon*** and the clade including *Peradectes* and members of the Ameridelphia and Alphadelphia is more problematic, and the classification of these three taxa involves the necessary arbitrary decisions mentioned at the beginning of this chapter. The cohorts Ameridelphia and Australidelphia were originally erected by Szalay (1982a), with Late Cretaceous marsupials, including *Alphadon* s.l., being assigned to the Ameridelphia. A recent classification (Marshall et al., 1990) has separated taxa like *Alphadon* s.l. and *Peradectes*, and assigned them to the Cohort Alphadelphia, emphasizing the separtation of these taxa from the Ameridelphia and Australidelphia. The analysis presented in Chapter 4 suggested that *Peradectes* was more closely related to these latter two cohorts, but did support the separation of *Alphadon* s.l. from these.

Both the Ameridelphia and Australidelphia are taxonomically diverse, and are separated from ***Turgidodon*** and ***Alphadon* s.s.*** by a large number of synapomorphies. As well, in **Figure 30**, character **8** (position of cusp C relative to the edge of the stylar shelf) separates ***Turgidodon*** and ***Alphadon* s.s.*** from the clade including members of the Ameridelphia (including *Peradectes*) and Australidelphia. All these suggest that ***Alphadon* s.s.*** be classified with ***Turgidodon***, rather than classifying either taxon with the latter clade. Given the topology of the consensus cladogram in **Figure 26**, this decision appears to be somewhat arbitrary, and the classification of these taxa does not follow directly (a one-to-one correspondence) from the cladogram. The separation of the clade including members of the Ameridelphia and Australidelphia from ***Turgidodon*** and ***Alphadon* s.s.*** on the basis of a large number of synapomorphies and greater taxonomic diversity in the former two taxa suggests that this classification is attempting to include some degree of evolutionary information. This was not deliberate, but followed from a desire to produce a somewhat conservative classification; it is more appropriate to classify ***Turgidodon*** and ***Alphadon*** **s.s.*** together as former members of the Genus *Alphadon* s.l. (and the Subfamily Alphadontinae) rather than to classify either of these genera with members of the Ameridelphia and Australidelphia. The other alternative would be to classify ***Turgidodon*** and ***Alphadon*** **s.s.*** separately, and at the same indentation in the classification as the Ameridelphia and Australidelphia. This would tend to emphasize a separation between ***Turgidodon*** and ***Alphadon*** **s.s.*** that I do not believe exists. Therefore, ***Alphadon*** **s.s.*** and ***Turgidodon*** are classified together and assigned to the **Alphadontinae***. The Subfamily Alphadontinae was first erected by Marshall et al. (1990) to include their *Alphadon* s.s. (minus "*Alphadon creber*") and *Albertatherium*. *Albertatherium* is an unusual genus, and other than the presence of a large stylar cusp C on referred upper molars, is not morphologically similar to any species of *Alphadon* s.l. Therefore, *Albertatherium* is not retained in the **Alphadontinae***, which is now restricted to ***Turgidodon*** and ***Alphadon*** **s.s.***. The designation of the **Alphadontinae*** reflects the polytomous arrangement of the groups in this metataxon, and from the classification (level of subordination), **Alphadontinae*** is the sister taxon to the Ameridelphia (including *Peradectes*) and Australidelphia.

NEW TAXON B
ALPHADONTINAE*
TURGIDODON Cifelli, 1990a

Type species. *Turgidodon praesagus* (Russell, 1952)

Included species. Type species, and *Turgidodon russelli*, *T. praesagus*, *T. rhaister*, *T. lillegraveni*, *T. madseni*, *T. petiminus*.

Distribution. Oldman Formation, Alberta; Judith River Formation, Montana; "Mesaverde" Formation, Wyoming; Kaiparowits Formation, Utah; Frenchman Formation, Saskatchewan, Judithian and Lancian NALMAs.

Revised diagnosis. See Cifelli, 1990a; also, trigon basin shallow; stylar cusp B, paracone, and paracone approximately subequal in height; cusp B hypertrophied, inflated labially, internal conular cristae high and wall-like, protocone anteroposteriorly expanded, protoconular cristae frequently present.

ALPHADON S.S.* Simpson, 1927

Type species. *Alphadon marshi* Simpson, 1927.

Included species. Type species, and *A. jasoni*, *Alphadon* sp. cf. *A. jasoni*, *A. halleyi*.

Distribution. Oldman Formation, Alberta; Judith River Formation, Montana; "Mesaverde" Formation, Wyoming; lowermost Kirtland Shale (Kirtland Formation), New Mexico; Kaiparowits Formation, Utah (Judithian NALMA); Lance Formation, Wyoming; Scollard Formation, Alberta; Frenchman Formation, Saskatchewan; Hell Creek Formation, Montana; Kirtland Formation, New Mexico (Lancian).

Discussion. Because the relationships of the three taxa assigned to ***Alphadon* s.s.*** are resolved as a polytomy along with *Turgidodon* and the clade including the more derived marsupial taxa, there are no character states (synapomorphies) unique to ***Alphadon* s.s.*** that are not shared by either one of these other taxa. Several characters were described in Chapter 4 that separated the members of the major polytomy, including ***Alphadon* s.s.***, from the taxa at the next most inclusive node, "**new genus B***" ("*Alphadon*" *creber* and "*Alphadon*" sp. cf. "*A.*" *creber*). Character **8**, the position of stylar cusp C relative to the edge of the stylar shelf, was described as a synapomorphy for ***Alphadon* s.s.*** and *Turgidodon*, not shared by members of the more derived marsupial clade. Members of the *Turgidodon*, *A. halleyi*, *A. marshi* and *A. jasoni* polytomy possess upper molars on which cusp C is more lingually placed, while all other taxa (including the more derived marsupial taxa) possess upper molars on which cusp C is more labially placed along the edge of the stylar shelf. The status of *Alphadon attaragos* was briefly discussed in Chapter 3, and for various reasons, was not included in this phylogenetic analysis. It was suggested that upper molars referred to *A. attaragos* (Cifelli, 1990a; **Plate 20E**) were morphologically similar to upper molars referred to *A. halleyi*. If further study indicates that the referral of these upper molars is correct, then *A. attaragos* would likely be included in ***Alphadon* s.s.***, and would perhaps be found to be most closely related to *A. halleyi*, giving some resolution to this metataxon.

The use of the metataxon convention with regards to ***Alphadon* s.s.*** is useful because it separates these species from *Turgidodon* and other species previously referred to *Alphadon* s.l., but still suggests that there may be some relationship between *A. halleyi*, *A. marshi* and *A. jasoni* that is not suggested by the character evidence at hand. The other alternative in this classification would be to restrict *Alphadon* s.s. to *A. marshi*, the original type species (Simpson, 1927), and to classify "*A.*" *halleyi* and "*A.*" *jasoni* in new genera within the larger polytomy. This would emphasize a separation between these species that likely does not exist, and may create unnecessary taxonomic confusion. To avoid these problems, *A. halleyi, A. marshi* and *A. jasoni* are retained in ***Alphadon* s.s.***.

THE COHORT ALPHADELPHIA AND THE FAMILY PERADECTIDAE. The use of **Alphadontinae*** allows ***Turgidodon*** and ***Alphadon* s.s.*** to be separated from the more derived marsupial taxa, including *Peradectes* and members of the cohorts Ameridelphia and Australidelphia (Szalay, 1982). Members of these two cohorts were included in this phylogenetic analysis (*Peratherium, Ankotarinja* and *Andinodelphys*), and form a monophyletic clade along with *Peradectes* (though the distribution of taxa does not exactly correspond to their previous classifications in the Ameridelphia (*Peratherium*) and Australidelphia (*Andinodelphys* and *Ankotarinja*); this is due, no doubt, to the limited number of taxa included from each of these higher-level taxa and the absence of diagnostic characters for these groups (tarsal characters for the Australidelphia; sperm pairing for the Ameridelphia) in the analysis). This monophyly is supported by several synapomorphies, listed in Chapter 4, and mapped on **Figure 30**. *Peradectes* was assigned with *Alphadon* s.l. (and several other marsupial taxa) to the Cohort Alphadelphia by Marshall et al. (1990); this reflects and expands upon the classification of *Peradectes* with *Alphadon* s.l. by Crochet (1979, 1980) in the Tribe Peradectini and by Reig et al. (1985, 1987) in the Family Peradectidae. The topology of the cladogram in **Figure 26** suggests that *Peradectes* does not share a closest relationship with species previously referred to *Alphadon* s.l., and should instead be assigned to the Cohort Ameridelphia (disregarding the position of *Ankotarinja* in **Figure 26**). This follows earlier suggestions by Krishtalka and Stucky (1983a) and Montellano (1986).

However, this interpretation does differ from that of Marshall et al. (1990a), and the validity of the Cohort Alphadelphia and the Family Peradectidae need to be discussed in greater detail. Three subfamilies were classified in the Cohort Alphadelphia, Order Peradectia, Family Peradectidae; Caroloameghiinae (*Caroloameghinia* Ameghino, 1901, *Roberthoffstetteria* Marshall, de Muizon and Sige, 1983, and *Glasbius* Clemens, 1966), Alphadontinae (*Alphadon* s.s. and *Albertatherium*) and Peradectinae (*Peradectes, Alleoedectes* Russell, 1984, *Armintodelphys* Krishtalka and Stucky, 1983a, *Kassinerotherium* Crochet, 1986, *Mimoperadectes* Bown and Rose, 1979). The Cohort Alphadelphia is generally similar in composition (except for the inclusion of the Subfamily Caroloameghiinae) to the original Tribe Peradectini (Crochet 1979, 1980) and the Family Peradectidae (Reig et al., 1987) in that referrals to these three groups were made because assigned taxa lacked synapomorphies characterizing more derived marsupial taxa (i.e., in the Tribe Didelphini, Family Didelphidae, or the Superfamily Didelphoidea). The lack of any synapomorphy supporting the Cohort Alphadelphia is seen on the cladogram presented by Marshall et al. (1990a: fig. 2), and taxa were said to be included in the Cohort Alphadelphia because they lacked the synapomorphies characterizing the cohorts Ameridelphia and Australidelphia. However, on this cladogram, the Family Peradectidae possesses one synapomorphy, the presence of stylar cusp C on the upper molars, with this state being convergently acquired within the Ameridelphia and Australidelphia. The Family Peradectidae (or the Tribe Peradectini) had not been previously supported by any synapomorphies.

Marshall et al. (1990a) resolved some of the variation observed within *Alphadon creber* (Fox, 1971) by dividing this species into *A. creber* [-C] and *A. creber* [+C]. *Alphadon creber* [-C] was separated from other taxa assigned to the Cohort Alphadelphia and was assigned to "Peradectoidea *incertae sedis*". The taxon "Peradectoidea *incertae sedis*" was included in the cladogram of Marshall et al. (1990: fig. 2) as "Plesion I.S.", and was resolved as the sister taxon to the Family Peradectidae. Since taxa assigned to the "Peradectoidea *incertae sedis*" lacked a stylar cusp C, the presence of a stylar cusp C would be a synapomorphy grouping the remaining taxa classified in the Cohort Alphadelphia (assigned to the Family Peradectidae), being convergently acquired within the Cohorts Ameridelphia and Australidelphia.

The use of the Cohort Alphadelphia and the monophyly of the Family Peradectidae as discussed by Marshall et al. (1990) are not supported by the results of the phylogenetic analysis presented in Chapter 4. *Peradectes* is more closely related to taxa in the Cohort Ameridelphia, and likely all members of the Subfamily Peradectinae should be assigned to this cohort. Since taxa in the other two subfamiles were referred to the Cohort Alphadelphia on the basis of a lack of synapomorphy, there is no evidence for retaining this cohort in a classification. The resolution of *Alphadon creber* s.l. given by Marshall et al. was criticized in Chapter 3, and characters other than the presence or absence of stylar cusp C were used to resolve this species by dividing it into two taxa, both characterized by the variable presence of this cusp. The phylogenetic analysis performed resulted in these two taxa being removed from *Alphadon* s.s., and also resulted in the character state "stylar cusp C consistently present" being a synapomorphy grouping taxa included in the major polytomy in **Figure 26**, including taxa assigned by Marshall et al. (1990) to the Cohorts Alphadelphia (*Peradectes* and their *Alphadon* s.s. (generally equal to ***Turgidodon*** and

Alphadon* s.s., as used in this analysis)), Ameridelphia (*Peratherium*), and Australidelphia (*Ankotarinja* and *Andinodelphys*). Therefore, the presence of stylar cusp C is **not** a synapomorphy of the Family Peradectidae, and convergently acquired in the cohorts Ameridelphia and Australidelphia (though this may not be strictly correct for the Australidelphia; on the cladogram presented by Marshall et al. (1990), the Order Microbiotheria is assigned to the Australidelphia and is the basalmost taxon within this cohort. Stylar cusp C is absent within the Order Microbiotheria (except for *Pediomys elegans*), and therefore, a consistently present stylar cusp C (in the form of two small stylar cusps) would be convergently acquired within the Australidelphia).

If the Cohort Alphadelphia is rejected and the presence of stylar cusp C is not a synapomorphy for the Family Peradectidae, then the status of these taxa is indeed similar to the Peradectini (Crochet, 1979, 1980) and Peradectidae (Reig et al., 1985, 1987). This analysis has indicated that *Peradectes* and *Alphadon* s.l. are not closely related, rather that *Peradectes* is more closely related to members of the Ameridelphia, like *Peratherium*. New hypotheses regarding the relationship of species assigned to *Alphadon* s.l. have also been suggested. ***Turgidodon*** and ***Alphadon* s.s.***are classified in the metataxon **Alphadontinae*** to reflect their relationships to taxa assigned to the cohorts Ameridelphia and Australidelphia (all of which are assigned to the **new taxon B**). ***Turgidodon*** and ***Alphadon* s.s.*** are not retained in a revised [meta]taxon Alphadelphia, even though this classification might adequately portray the relationships of ***Turgidodon***, ***Alphadon* s.s.*** and all other taxa assigned to the Alphadelphia to members of the cohorts Ameridelphia and Australidelphia. As suggested earlier, the Alphadelphia (and the Peradectini and Peradectidae) are not defined by any synapomorphy, and seem to have persisted only because of uncertainties regarding the relationships of the included taxa. Future studies should be directed towards resolving, rather than maintaining, these relationships.

TABLE 1. A comparison of **A**: anteroposterior lengths and transverse widths for upper and lower molars ("width" = trigonid width) referred to "*Alphadon*" *praesagus* (from the Oldman Formation, Alberta, and Judith River Formation, Montana, taken from Russell, 1952 and Sahni, 1972: table 1, respectively), **B**: "*Alphadon*" *russelli* (from the Oldman River Formation, taken from Fox, 1979: table 2), **C**: Measurements of "*Alphadon*" *russelli* from the "Mesaverde" Formation (taken from Lillegraven and McKenna, 1986) and **D:** the Judith River Formation (taken from Montellano, 1986).

A

"*Alphadon*" *praesagus* (Oldman Formation)

Molar	**Length (X:no. of specimens)**	**Width (X:no.of specimens)**
m3	3.3 mm: 1	2.2 mm: 1

"*Alphadon*" *praesagus* (Judith River Formation)

Molar	**Length (X:no. of specimens)**	**Width (X:no.of specimens)**
M1	2.6: 2	2.65: 1
M2	2.25: 1	2.75: 1
M3	2.3: 1	3.4: 1
m1	2.55: 2	1.6: 1
m2	2.8: 4	1.67: 4
m3	1.9: 2	1.7: 2

B

"*Alphadon*" *russelli* (Oldman Formation)

Molar	**Length (X:no.of specimens)**	**Width (X:no. of specimens)**
M1	2.6: 7	2.6: 5
M2	2.8: 5	2.9: 4
M3	2.7: 8	3.3: 7
m1	2.5: 24	1.3: 24
m2	2.8: 22	1.8: 21
m3	3.0: 16	1.8: 15

C

"*Alphadon*" *russelli* ("Mesaverde" Formation)

Molar	**Length (X:no. of specimens)**	**Width (X:no. of specimens)**
M1	--	2.72: 1 (anterior width)
M2	2.65: 5	3.06: 5
M3	2.41:1	3.17:1

TABLE 1 continued

m3	2.96: 1	1.53: 1

D **"*Alphadon*" *russelli* (Judith River Formation)**

Molar	**Length (X:no. of specimens)**	**Width (X:no. of specimens)**
M1	2.66:1	2.84:1
M2	2.83:1	2.9: 2
M3	3.35:1	2.38:2
m1	2.45: 5	1.22: 5
m2	2.78: 11	1.65: 11
m3	2.95: 3	1.69: 3

TABLE 2. Molar measurements (mm) for *Alphadon jasoni* and *Alphadon* sp., cf. *A. jasoni*, M1-M3: anterior-posterior length (**AP**); anterior width (**AW**); posterior width (**PW**); buccolingual length (**BL**, Storer, 1991).

Upper molar measurements (mm.) for *Alphadon jasoni*.

M1s

		AP	AW	PW	BL
Scollard Formation					
UALVP	2316	2.085	1.851	2.089	
	2221	2.037	2.163	2.471	
	2738	2.144	2.074	2.238	
	3945	2.110	2.032	2.282	
	2994	2.427	2.484	2.810	
	4023	2.007	2.123	2.297	
	2822	1.891	1.992	2.211	
	2473	2.141	1.928	2.275	
	3806	1.851	1.847	2.030	
	2728	2.003	1.747	2.067	
Frenchman Formation					
UALVP	22678	2.311	2.077	2.487	
	22679				
	22689	2.274	2.364	2.530	
	22683	2.029	2.043	2.327	
	22681	-------	1.873	2.121	
P	1927.49	1.98			2.15
	1927.190	2.14			2.42
	1927.73	2.17			2.55
	1927.742	2.00			2.15
	1927.735	2.01			2.31

M2s

		AP	AW	PW	BL
Lance Formation					
YPM	13655	2.217	2.396	2.546	
Scollard Formation					
UALVP	2221	2.037	2.163	2.471	
	3956	1.924	2.111	2.257	
	2313	2.228	2.201	2.323	
	2309	2.295	2.341	2.517	
	2219	2.331	2.574	2.718	

TABLE 2 continued

UALVP	3668	2.133	2.207	2.393	
	3151	2.181	2.489	2.660	
	3740	1.998	2.000	2.252	
M2s					
UALVP	3241	2.200	2.449	2.602	
	2814	2.166	2.455	2.520	
Frenchman Formation					
P	2004.4	2.12			2.48
	2004.68	2.07			2.30
	1927.74	2.02			2.44
	1927.660	2.12			2.60
	1927.677	1.83			------
	2004.83	2.09			------
Fruitland/transitional Kirtland Formations					
UNM-B	1743	2.20			
M3s					
Scollard Formation					
UALVP	4014	2.190	-------	-------	
	3708	1.992	-------	-------	
Frenchman Formation (Wounded Knee local fauna)					
UALVP	22691	2.163	2.624	2.610	
	22269	2.242	2.938	2.933	
	22694	2.401	2.903	2.974	
	22693	2.172	2.541	2.526	
	22696	2.004	-------	-------	
	22695	2.138	-------	-------	
(Gryde locality)					
P	1927.91	2.35			2.61
	1927.61	2.19			2.48
	2004.12	2.25			-----
	1927.695	2.19			2.64
	1927.504	2.00			2.45
	1927.481	2.03			-----
	1927.460	2.33			-----
	1927.107	1.99			2.70
Lance Formation					
UCMP	51385	2.531	2.572	2.747	

TABLE 2 continued

Upper molar measurements (mm.) for *Alphadon* sp., cf. *A. jasoni*.

	AP	AW	PW
M1 Scollard Formation			
UALVP 2901	2.482	-------	-------
2900	2.413	2.534	2.758
2982	2.578	2.615	2.899
4071	2.626	2.472	2.784
2815	2.611	2.667	2.902
2545	2.641	2.568	2.867
2846	2.606	2.605	2.931
M2			
UALVP 2758	3.011	3.263	3.453
2621	2.946	3.157	3.293
2452	3.003	3.075	3.217
2846	2.906	3.225	3.345
M3			
UALVP 2846	2.635	3.368	3.519

TABLE 3. Upper molar measurements (mm.) for M1-3 of *Didelphis virginiana*, taken from both male and female specimens, collected from across the United States. Symbols given beside catalogue numbers for M3s (but applicable to the M1s and M2s) are as follows: **(M)**- male; **(F)**- female; **(X)**- sex unknown.

M1s

	anteroposterior length	**anterior width**	**posterior width**
UM			
87099	4.577	3.030	4.357
95820	5.175	4.277	5.152
164970	5.336	4.396	5.407
164969	4.919	4.458	6.270
42370	5.095	4.477	5.938
3833	5.229	4.590	6.002
122350	5.111	4.588	6.131
112349	5.018	4.263	5.730
112348	5.213	4.619	6.140
112351	5.142	4.421	5.976
11219	5.470	4.649	6.289
USNM			
395546	4.910	4.389	5.572
395541	5.537	4.593	5.743
291196	4.872	4.189	5.471
261193	4.906	4.164	5.583
261174	4.858	4.152	5.490
236639	5.329	4.155	5.164
395542	4.740	4.186	5.451
300673	5.059	4.367	5.628
238062	5.480	4.767	6.341
337109	5.061	4.494	5.611
395540	5.521	4.655	6.020
313788	5.663	4.559	5.822
337017	5.119	4.195	5.599
395545	4.569	4.014	5.372
395536	5.115	4.424	5.686
347671	5.515	4.452	4.688
347673	4.928	4.117	5.234
337108	5.151	4.547	6.324
347669	5.621	4.749	6.049
UK			
45187	4.520	4.208	5.508
40788	4.987	4.028	4.966
9121	5.072	4.161	5.304
79418	5.003	4.169	5.436

TABLE 3 continued

3607	4.857	4.489	5.919
121908	5.015	4.227	5.385
UK			
3605	4.579	4.111	5.376
4763	5.214	5.658	4.483
9120	5.002	4.195	5.790
8975	5.748	4.878	5.614
5522	4.922	4.229	5.461
12783	4.744	4.402	5.547
5616	4.858	3.701	5.362
40181	4.817	4.329	5.809
3608	5.177	4.175	5.290
3970	4.791	4.498	5.886
22041	4.947	4.320	5.578
MCZ			
8480	5.036	4.678	3.810
52762	4.872	3.387	5.111
B1921	4.920	3.920	5.461
4950	5.354	4.256	5.644
32208	5.341	4.634	5.518
B2880	5.118	4.447	5.532
10611	5.178	4.015	5.437
32209	5.103	4.408	5.797
43040	5.103	4.408	5.797

M2s

	anteroposterior length	**anterior width**	**posterior width**
UM			
87099	5.421	4.692	5.967
95820	5.725	4.988	6.127
164970	5.838	5.091	6.424
164969	5.774	5.778	7.112
42370	5.844	5.27	7.199
3833	5.840	5.369	7.366
122350	5.761	5.157	7.246
112349	5.466	5.029	6.712
112348	5.792	5.291	7.239
112351	5.480	5.399	7.625
11219	5.836	5.658	7.771
USNM			
395546	5.793	5.381	6.747
395541	5.879	5.484	6.962

TABLE 3 continued

291196	5.317	4.913	6.673
261193	5.692	5.212	6.695
USNM			
261194	5.968	5.227	6.819
347672	6.064	5.639	7.337
236639	5.934	5.235	6.516
395542	5.400	4.579	4.579
300673	5.929	5.012	6.786
238062	5.747	5.438	6.761
337109	5.879	5.207	6.810
395540	6.329	5.69	7.446
313788	6.250	5.899	7.712
337017	5.402	4.988	6.935
395545	5.387	4.603	6.251
395536	5.169	4.886	6.654
347671	6.391	5.527	6.412
347673	5.782	5.056	6.349
337108	6.361	5.476	6.999
347669	6.561	5.876	7.320
UK			
45187	4.724	4.576	6.431
40788	5.652	5.028	6.319
9121	5.630	4.941	6.482
79418	5.633	5.041	6.601
3607	5.287	5.029	7.009
79419	5.737	5.208	6.712
121908	5.329	5.037	6.607
3605	4.989	4.837	6.641
4763	5.999	5.223	7.138
9120	6.022	5.37	7.153
8975	6.398	5.706	7.465
5522	5.558	5.031	6.671
12783	5.857	5.271	7.278
5616	5.429	4.798	6.843
40181	5.891	5.191	7.171
3608	5.542	5.237	7.097
3970	5.509	5.49	6.965
22041	5.765	5.067	6.842
MCZ			
8480	5.592	4.638	5.833
52762	5.719	4.861	6.237
B1921	5.780	4.748	6.361
4950	5.887	5.230	6.903
32208	5.759	6.321	6.554
B2880	6.050	5.474	6.765

TABLE 3 continued

10611	5.953	5.123	6.259
32209	6.169	6.199	7.763
43040	6.126	5.450	6.756

M3s

	anteroposterior length	**anterior width**	**posterior width**
UM			
87099 (F)	5.869	5.448	7.192
95820 (M)	6.768	6.353	7.284
164970 (M)	6.273	5.998	7.305
164969 (M)	6.335	6.511	8.279
42370 (F)	6.194	6.508	8.425
3833 (M)	6.031	6.261	8.098
122350 (M)	6.346	6.223	7.797
112349 (F)	5.530	5.890	7.547
112348 (M)	6.033	6.205	8.501
112351 (X)	6.239	6.311	8.551
USNM			
395546 (X)	6.228	6.195	7.540
395541 (X)	6.877	6.323	8.042
291196 (X)	6.214	5.893	7.484
261193 (X)	5.634	5.868	7.777
261194 (X)	6.246	6.343	7.940
347672 (M)	6.427	6.621	8.473
236639 (X)	•	5.947	7.616
395542 (X)	5.521	5.372	7.101
300673 (M)	6.990	6.385	8.019
238062 (M)	6.136	6.574	8.147
337109 (X)	6.198	6.045	7.938
395540 (X)	6.435	6.050	7.827
313788 (M)	6.595	6.604	8.269
337017 (F)	5.832	5.575	7.512
395545 (X)	5.567	5.203	7.037
395536 (F)	5.788	5.840	7.812
347671 (F)	5.934	6.317	7.608
347673 (F)	6.187	5.889	7.445
337108 (F)	6.691	6.668	8.068
347669 (F)	6.707	6.163	8.37
UK			
45187 (F)	5.904	5.677	7.564
40788 (X)	5.940	5.798	7.389
9121 (M)	6.371	6.002	7.986
79418 (M)	6.314	6.387	8.045

TABLE 3 continued

3607 (F)	6.102	5.780	6.102
79419 (F)	5.499	5.605	7.021
121908 (F)	6.138	5.790	7.435

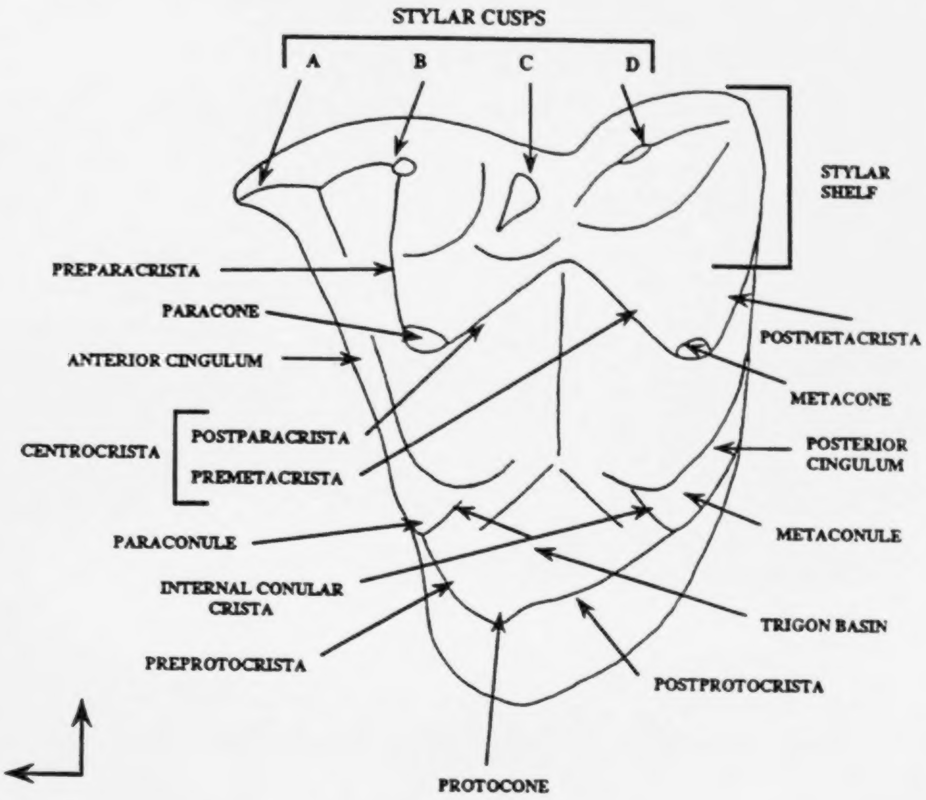
UK

3605 (F)	5.698	5.700	7.416
4763 (M)	6.523	6.335	8.135
9120 (M)	6.416	6.245	8.157
8975 (M)	6.768	6.875	8.837
5522(M)	5.758	5.867	7.369
12783 (F)	5.772	5.675	7.536
5616 (F)	5.768	6.148	8.137
40181 (M)	6.325	6.113	8.094
3608 (F)	5.729	6.060	7.924
3970 (M)	6.353	6.278	8.269
22041 (M)	•	6.240	8.110

MCZ

8480 (X)	6.259	5.349	7.024
52762 (F)	5.600	5.682	7.320
B1921 (M)	5.715	5.783	7.727
4950 (M)	6.323	6.181	7.561
32208 (M)	6.278	6.294	8.204
B2880 (M)	5.790	6.521	7.862
10611 (F)	6.444	5.991	7.804
32209 (M)	5.316	4.933	6.300
43040 (X)	6.224	6.137	7.731

Figure 1. Nomenclature of various morphological features of the occlusal surfaces of A) Upper and B) Lower molars referred to *Alphadon* s.l., as used in this study.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A
B
C
D
STYLAR SHELF
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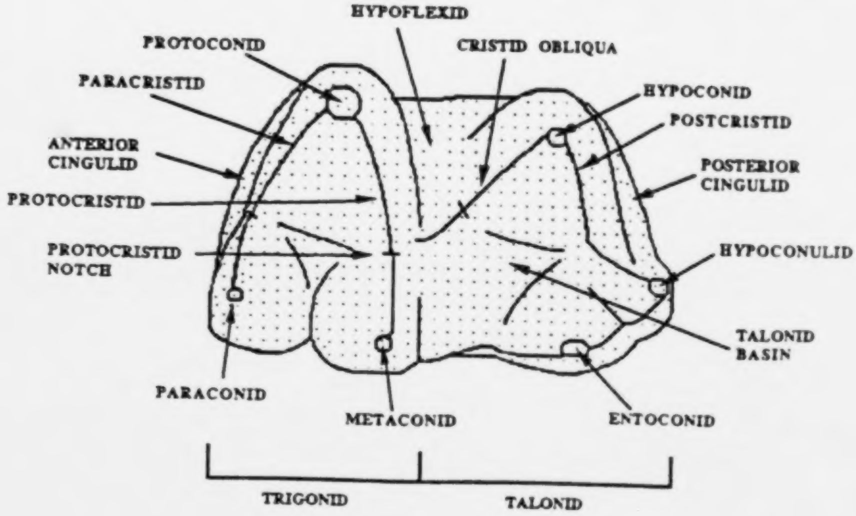
PARACONE
POSTMETACRISTA
ANTERIOR CINGULUM
METACONE
CENTROCRISTA
POSTPARACRISTA
PREMETACRISTA
POSTERIOR CINGULUM
PARACONULE
METACONULE
INTERNAL CONULAR CRISTA
TRIGON BASIN
PREPROTOCRISTA
POSTPROTOCRISTA
PROTOCONE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PROTOCONID
CRISTID OBLIQUA
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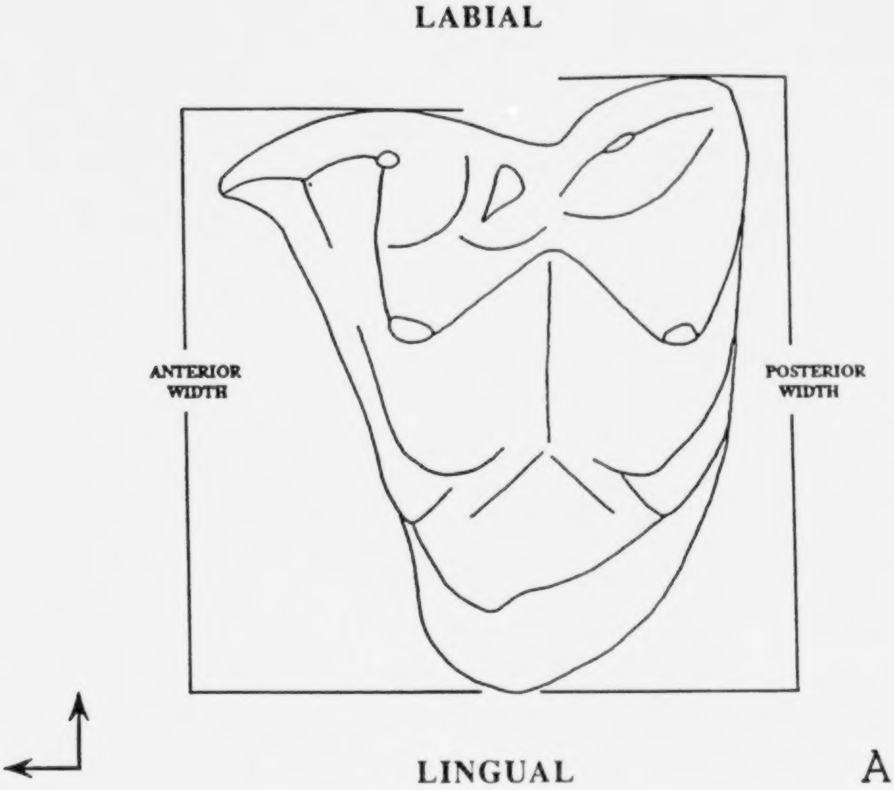
POSTCRISTID
ANTERIOR CINGULID
POSTERIOR CINGULID
PROTOCRISTID
PROTOCRISTID NOTCH
HYPOCONULID
TALONID BASIN
PARACONID
METACONID
ENTOCONID
TRIGONID
TALONID

Figure 2. Molar measurements used in this study. A) Upper molar: anterior and osterior width, measured transversely (labiolingually) across the tooth; B) Upper molar: length, measured anteroposteriorly across the tooth; C) Lower molar: transverse widths and anteroposterior lengths of the trigonid and talonid.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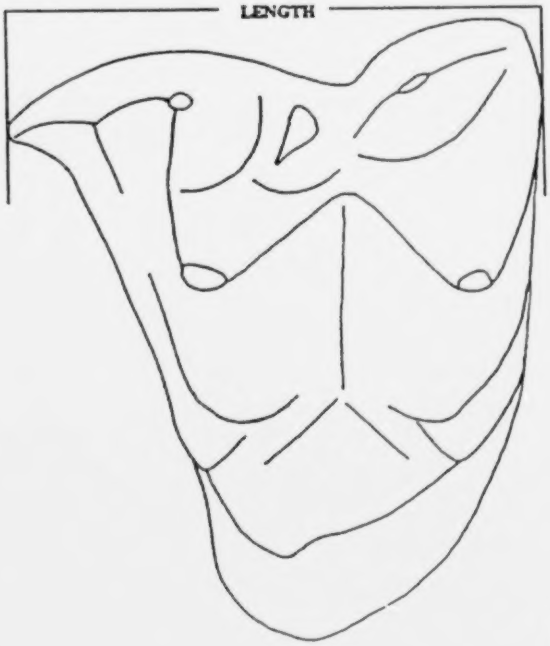
POSTERIOR WIDTH
LINGUAL

A



B

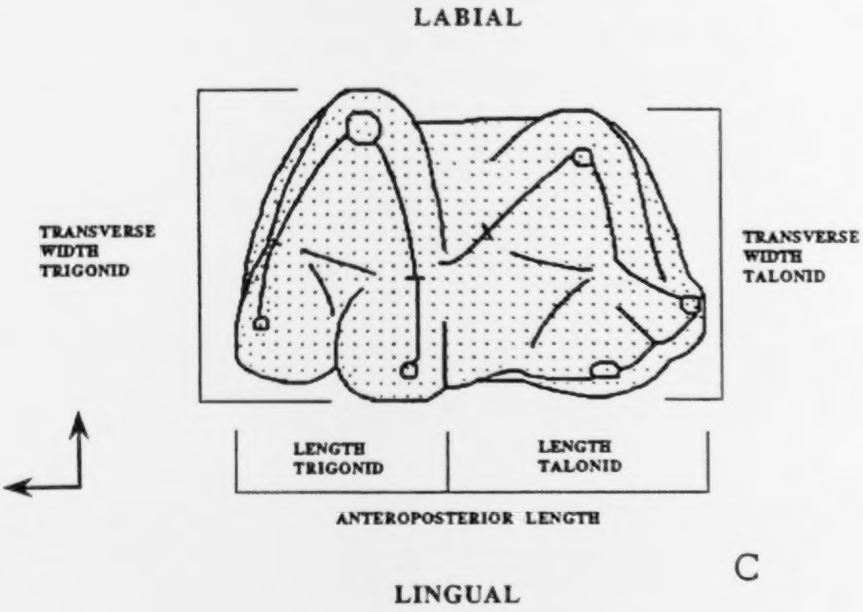
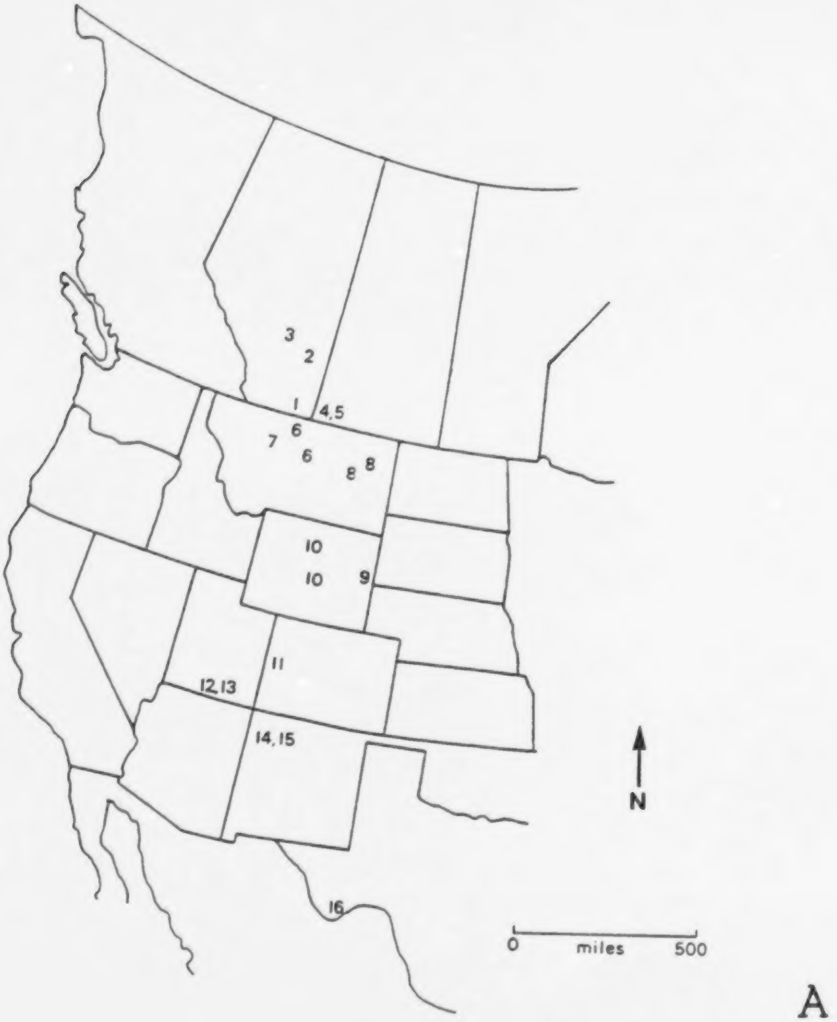

LABIAL
TRANSVERSE WIDTH TRIGONID
TRANSVERSE WIDTH TALONID
LENGTH TRIGONID
LENGTH TALONID
ANTEROPOSTERIOR LENGTH
C
LINGUAL

Figure 3. The geographical distribution of fossil mammal localities producing specimens referable to *Alphadon* s.l. across western North America. A) Geographical distribution; B) Localities and the NALMA to which species from these localities are referred.



LOCALITY	FORMATION	NALMA
1	Milk River; Alberta	Aquilan
2	Oldman; Alberta	Judithian
3	Scollard; Alberta	Lancian
4	Frenchman; Sask.	Lancian
5	Ravenscrag; Sask.	Lancian
6	Judith River; Montana	Judithian
7	Two Medicine; Montana	Judithian
8	Hell Creek; Montana	Lancian
9	Lance; Wyoming	Lancian
10	"Mesaverde"; Wyoming	Judithian
11	Williams Fork; Colorado	"Edmontonian"
12	Kaiparowits; Utah	Judithian
13	Wahweap; Utah	Aquilan
14	Kirtland; N. Mexico	Lancian
15	Fruitland/transitional & lower Kirtland; N. Mexico	"Edmontonian"
16	Aguja; Texas	Judithian

B

Figure 4. The distribution of various species referred to higher-level taxa (the majority previously referred to *Alphadon* s.l.), as described in Chapter 5, including the Late Cretaceous NALMA each is assigned to, and associated Late Cretaceous (Campanian and Maestrichtian) formations (adapted from Lillegraven and Ostresh, 1990: table 1).

STAGES	NALMA size of square not necessarily correlated with NALMA length	ASSIGNED SPECIES	ASSOCIATED FORMATIONS assigned species are not necessarily correlated with formations directly across from them
Maestrichtian	Lancian	_Alphadon* marshi_ _Alphadon* jasoni_ _Alphadon* sp., cf. A. jasoni_ _Turgidodon rhaister_ _Turgidodon petiminus_ _Protalphadon lulli_ _Protalphadon_ n. sp. A	Scollard, Alberta Ravenscrag, Saskatchewan Frenchman, Saskatchewan Hell Creek, Montana Lance, Wyoming Kirtland, New Mexico
Campanian	Edmontonian	_Alphadon* marshi_ _Alphadon* halleyi_	Fruitland/transitional and lower Kirtland, New Mexico
	Judithian	_Alphadon* halleyi_ _Alphadon* attaragos_ _Turgidodon madseni_ _Turgidodon lillegraveni_ _Turgidodon praesagus_ _Turgidodon russelli_	Oldman, Alberta Judith River, Montana Two Medicine, Montana "Mesaverde", Wyoming Kaiparowits, Utah
	Aquilan	new genus B* _creber_ new genus B* sp., cf. n. gen. B* creber new genus A new species A	Milk River, Alberta Wahweap, Utah

Figure 5. Various higher-level classifications of the Marsupialia, and the position of *Alphadon* s.l. in these classifications; A) From Simpson, 1929; B) From Hay, 1930; C) From Clemens, 1966; D) From Crochet, 1979, 1980; E) From Reig et al., 1985, 1987; F) From Aplin and Archer, 1987; G) From Marshall et al., 1990.

a) **ORDER MARSUPIALIA** Illiger 1811
- **Family Didelphidae Gray, 1821**
  - Subfamily Pediomyinae Simpson, 1927
  - **Subfamily Didelphodontinae** Simpson, 1929
    - ***Alphadon*** Simpson, 1927
  - Subfamily Microbiotheriinae Simpson, 1929
  - Subfamily Didelphiinae (Gray, 1821) Simpson, 1927

after Simpson, 1929

b) **ORDER MARSUPIALIA**
- **Family Didelphidae**
  - Subfamily Pediomyinae
  - **Subfamily Thlaeodontinae (Cope, 1892)**
    - ***Alphadon***
  - Subfamily Microbiotheriinae
  - Subfamily Didelphiinae

after Hay, 1930

c) **ORDER MARSUPIALIA**
- **Superfamily Didelphoidea (Gray, 1821) Osborn, 1910**
  - **Family Didelphidae**
    - **Subfamily Didelphinae Simpson, 1935**
      - ***Alphadon***
    - Subfamily Glasbiinae Clemens, 1966
    - Subfamily Microbiotheriinae
    - Subfamily Caroloameghiniinae Clemens, 1966
  - Family Pediomyidae (Simpson, 1927) Clemens, 1966
  - Family Stagodontidae Marsh 1889

after Clemens, 1966

d) **SUPER-ORDRE MARSUPIALIA**
- **ORDRE MARSUPICARNIVORA** Ride, 1964
  - **Super-famille Didelphoidea**
    - **Famille Didelphidae**
    - **Sous-famille Didelphinae**
      - **Tribe Peradectini** Crochet, 1979
        - ***Alphadon***
        - ***Albertatherium*** Fox, 1971
        - *?Bobbschaefferia* Paulo Couto, 1970
        - *Mimoperadectes* Bown and Rose, 1979
        - *Peradectes* Matthew and Granger, 1921
      - **Tribe Didelphini** Crochet, 1979

after Crochet, 1979, 1980

e) **Order Polyprotodonta** Owen 1866
- **Suborder Didelphimorpha** Gill 1842
  - **Superfamily Microbiotherioidea** (Ameghino 1887) n. rank
    - **Family Peradectidae**
      - ***Albertatherium***
      - *Alloeodectes* Russell 1984
      - ***Alphadon***
      - *Ankotarinja* Archer, 1976
      - *Bobbschaefferia*
      - *Garatherium* Crochet, 1984
      - *Mimoperadectes*
      - *Peradectes*
    - **Family Microbiotheriidae** Ameghino 1887
      - Subfamily Microbiotheriinae
      - Subfamily Glasbiinae
      - Subfamily Pediomyinae
    - **Family Caroloameghiniidae** Ameghino 1901
  - **Superfamily Didelphoidea**

after Reig et al., 1985, 1987

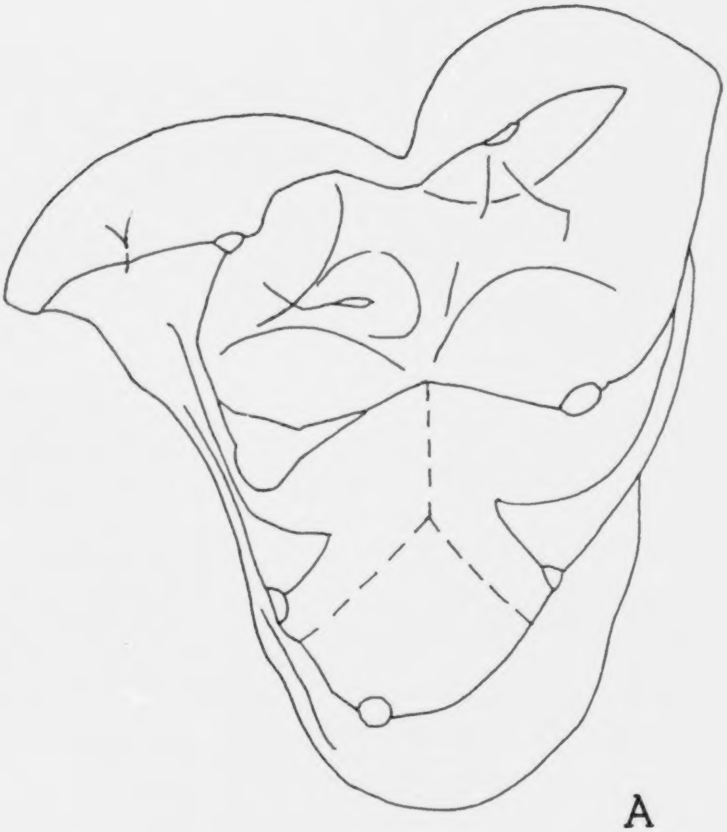
f) **SUPERCOHORT MARSUPIALIA** (Illiger, 1811) Cuvier, 1817
- **Cohort Ameridelphia** Szalay, 1982
- **Cohort Australidephia** Szalay, 1982
- **Cohort *incertae sedis***
- **Family Peradectidae** (Crochet, 1979) sedis mutabilis
  - ***Alphadon***
  - ***Albertatherium***
- **Family Stagodontidae** sedis mutabilis
- **Family Pediomyidae** sedis mutabilis

after Aplin and Archer, 1987

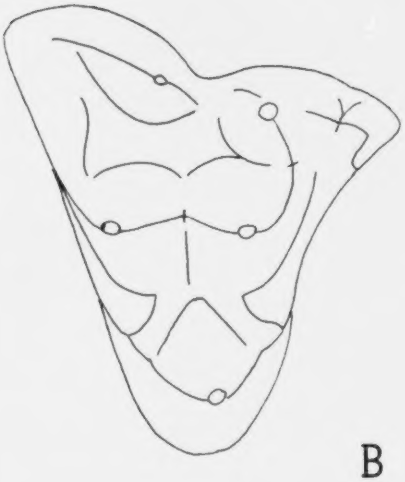
g) Cohort Ameridelphia
- Cohort Australidelphia
- **Cohort Alphadelphia** Marshall, Case and Woodburne, 1990
  - **Order Peradectia** Marshall, Case and Woodburne, 1990
    - **Superfamily Peradectoidea** Marshall, Case and Woodburne, 1990
      - **Family Peradectidae**
        - **Subfamily Alphadontinae** Marshall, Case and Woodburne, 1990
          - ***Alphadon***
          - ***Albertatherium***
        - **Subfamily Peradectinae**
          - ***"Alphadon" "creber"*** [+C]
          - *Alloeodectes*
          - *Armintodelphys* Krishtalka and Stucky 1983a
          - *Kasserinotherium* Crochet, 1986
          - *Mimoperadectes*
          - *Peradectes*
        - Subfamily Caroloameghiinae
    - **Peradectoidea *incertae sedis***
      - ***"Alphadon" creber*** [-C]

Marshall, Case and Woodburne, 1990

Figure 6. Comparison of the upper molar morphology of *Turgidodon rhaister* (formerly *Alphadon rhaister*) and *Alphadon* sp., cf. *A. creber* (formerly *A. creber*): A) Camera lucida drawing of the left M2 of UCMP 50292, holotype of *Turgidodon haister*, left maxillary fragment preserving M1-M3; B) Camera lucida drawing of UALVP 5541, RM2 of *Alphadon* sp., cf. *A. creber*. Scale = 1mm.

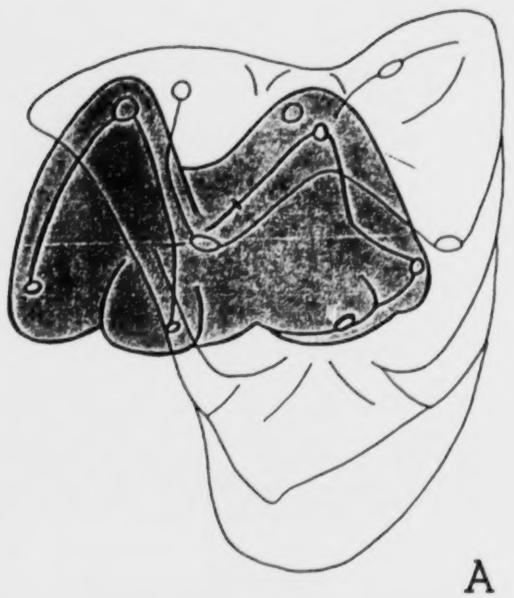


A

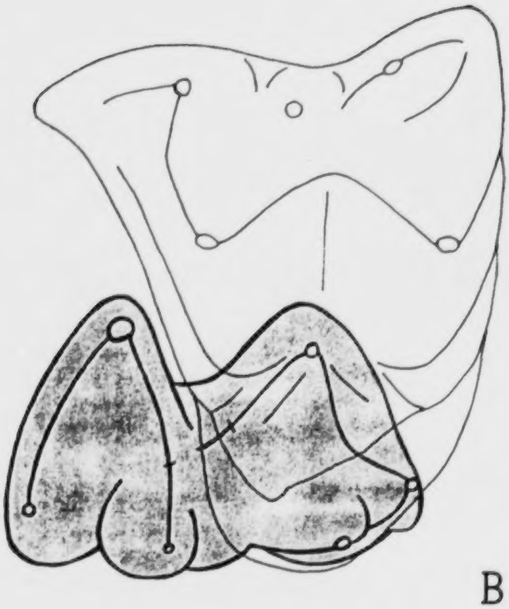


B

Figure 7. The position of a generalized marsupial lower molar (shaded) relative to the upper molar (unshaded) during two phases of the chewing cycle. A) Beginning of occlusion, and B) The end of the cycle, as the basined talonid comes to rest against the protocone of the upper. Between A) and B), the hypoconulid passes between the paracone and metacone, the posterior wall of the trigonid shears downward against the preparacrista, the anterior wall of the paracone and the anterior cingulum, and the front part of the trigonid shears against the postmetacrista (see also Crompton, 1971). Note the relationships of various upper and lower molar features to one another at each part of the cycle.



A



B

Figure 8. Morphological changes along the tooth row, from M1-M4. Camera lucida drawing of UALVP 2846, left maxillary fragment preserving M1-M4 (on the actual specimen, M4 is pushed down relative to the other molars; it has been reconstructed in this figure). Scale = 1mm.

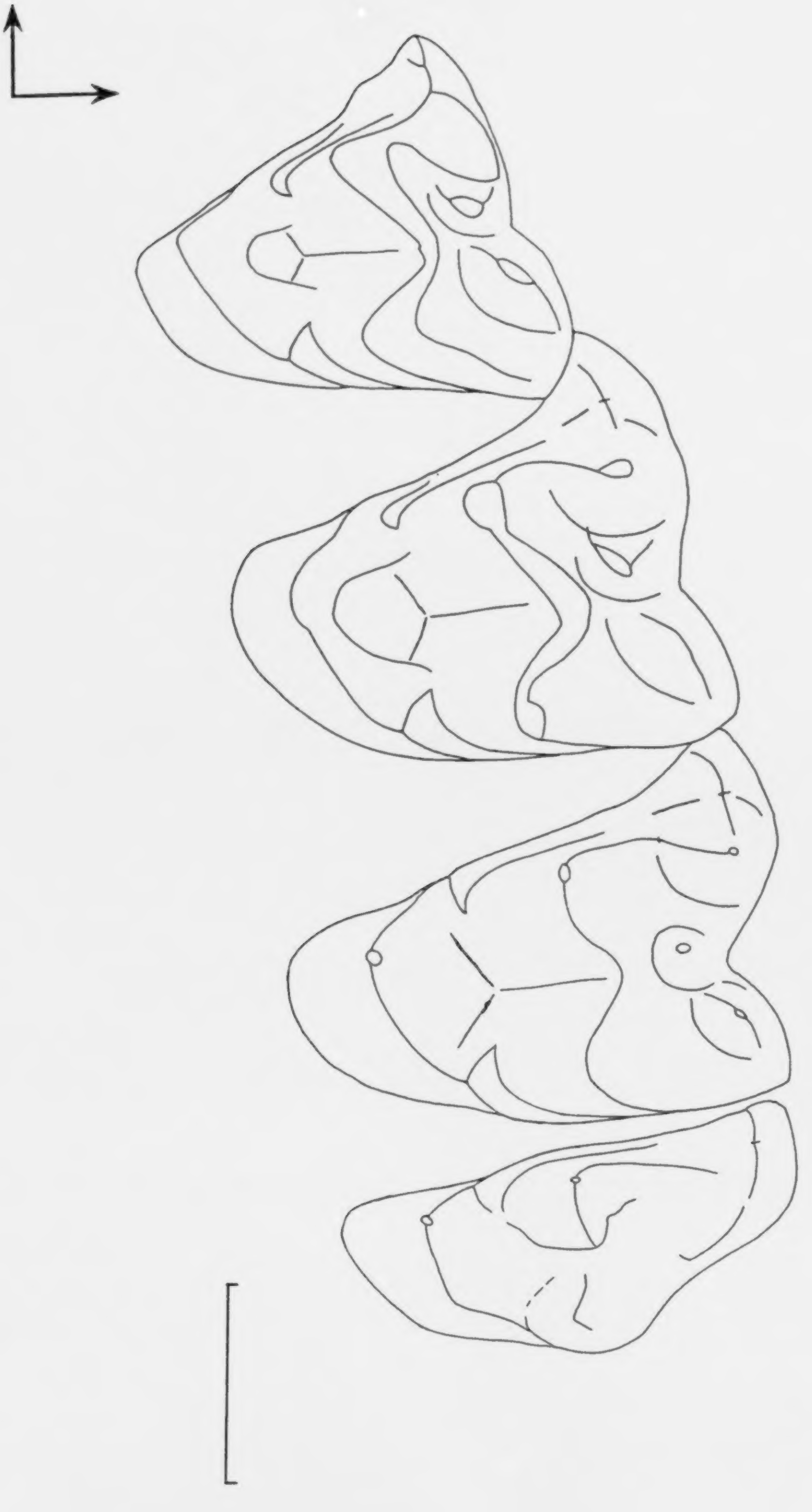
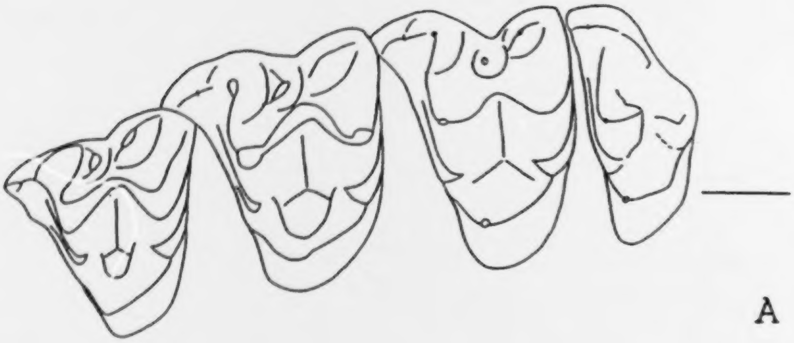
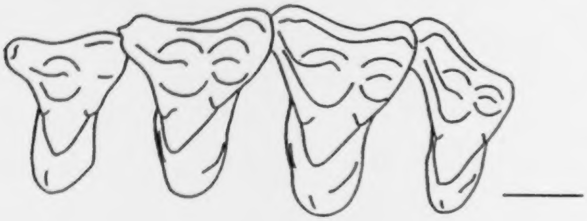


Figure 9. Comparisons of the overall shape of various upper molars between marsupials and eutherians: A) Camera lucida drawing of UALVP 2846, *Alphadon jasoni*, left M1-4; B) MgM-1/3 *Kennalestes gobiensis*, right P4, M1-3 (adapted from Kielan-Jaworowska et al., 1979: fig. 12-3A). Scale = 1mm.



A



B

Figure 10. A) Right upper molars of *Pappotherium pattersoni*- labial view of pentultimate and ultimate molars; B) Occlusal view of pentultimate molar. The dashed line indicates the position of the anteriormost end of the ultimate molar. C, E) Right upper molar of *Holoclemensia texana*, labial views of pentultimate and ultimate molars, respectively; D, F) occlusal views of pentultimate and ultimate molars, espectively. (Illustration from Lillegraven, et al., Mesozoic Mammals: The First Two-Thirds of Mammalian History, © 1979 The Regents of the University of California).

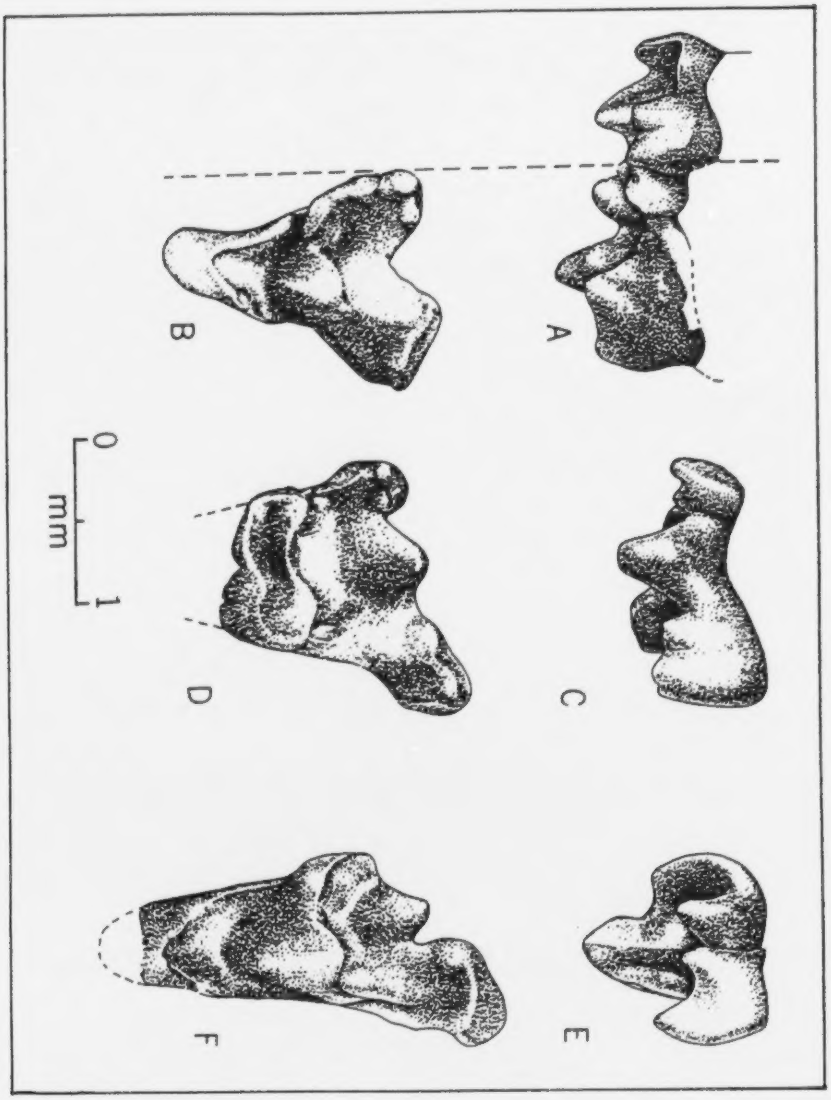
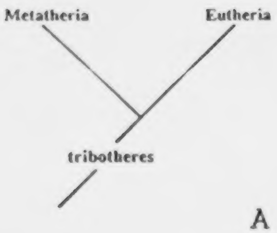
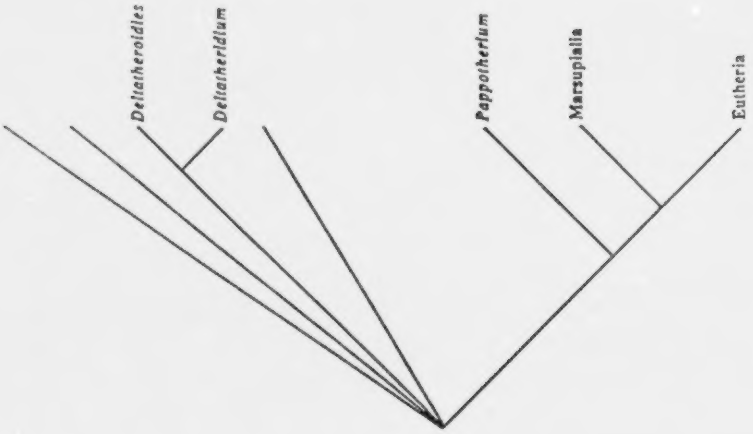

A
B
C
D
E
F
0
mm
1

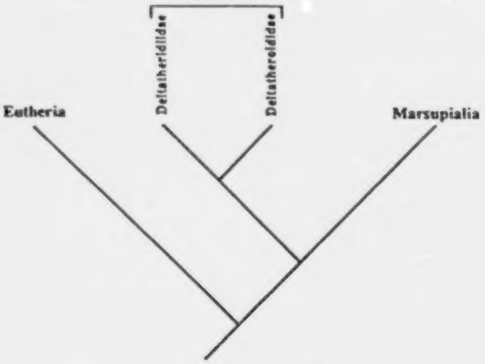
Figure 11. Various hypotheses of outgroup relationships to the Marsupialia: A) From Marshall et al., 1990; B) From Cifelli, 1990b; C) From Kielan-Jaworowska and Nessov, 1990.


Metatheria
Eutheria
tribotheres

A

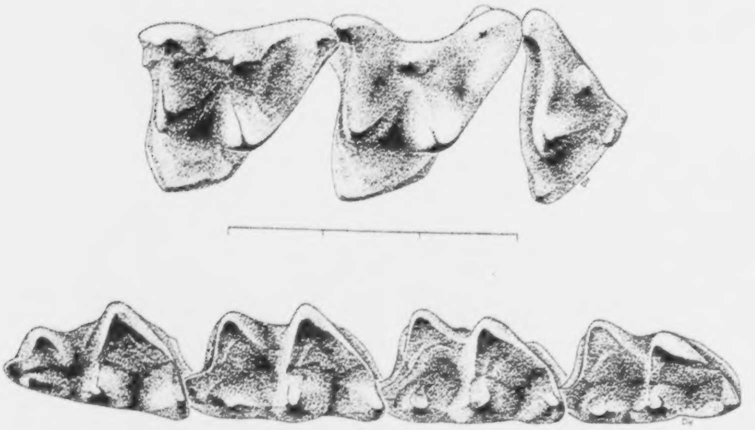

Deltatheroides
Deltatheridium
Pappotherium
Marsupialia
Eutheria

B


Deltatheroida
Deltatheridiidae
Deltatheroididae
Eutheria
Marsupialia

C

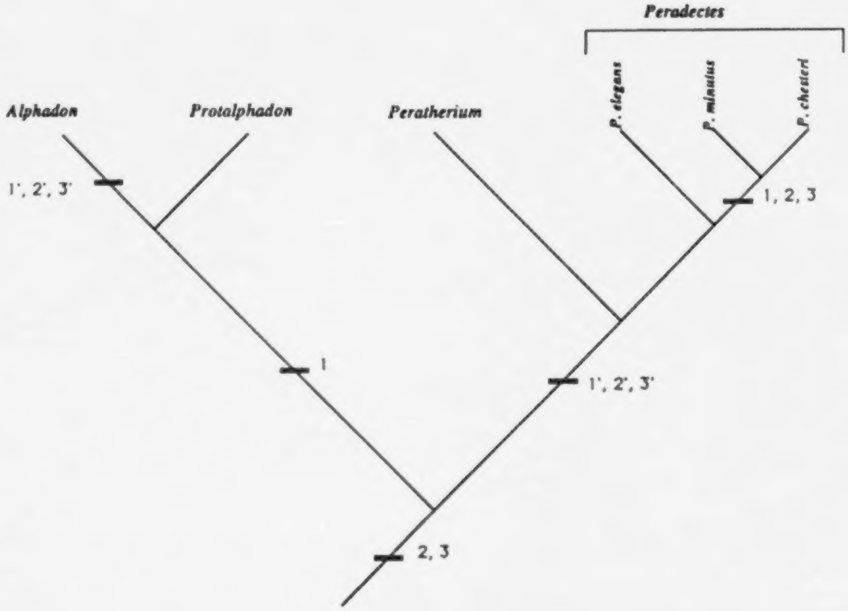
Figure 12. UALVP 8572, *Herpetotherium fugax*- A) Upper molars of UALVP 8572, M2-4; B) lower molars of UALVP 8572, m1-4 (from Fox, 1983: fig. 2a, b, used with permission of the publisher, Canadian Journal of Earth Sciences, entire scale= 3 mm; B) Lower molars of UALVP 2846, including part of m1 and m2-3, x 13. This specimen includes upper and lower molars found in occlusion.



A

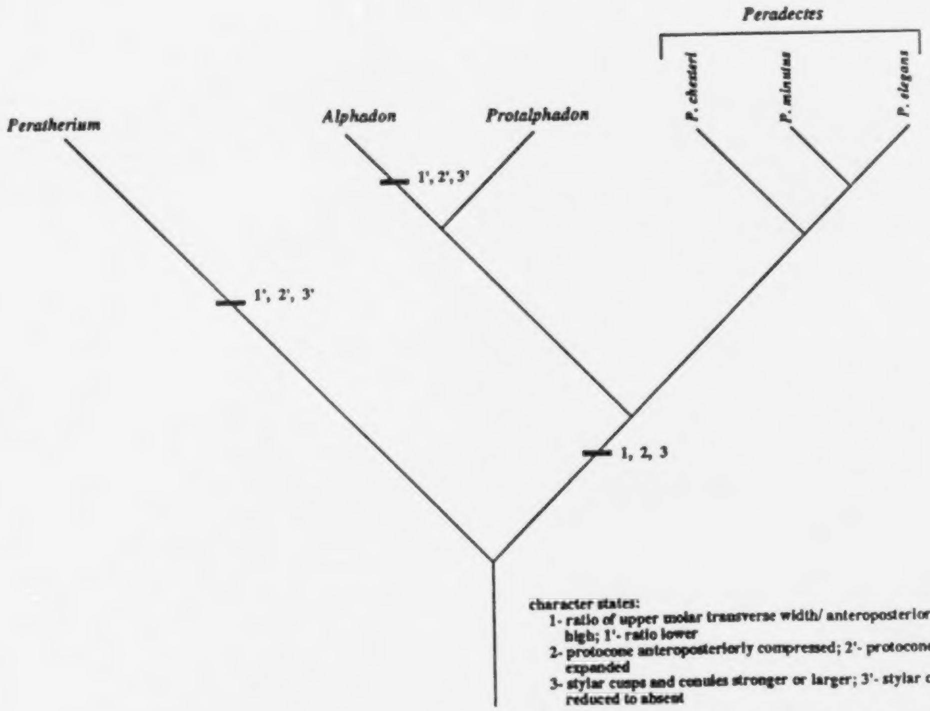
B

Figure 13. Various relationships when the most plesiomorphic taxon within *Peradectes* is changed. A) *Peradectes elegans* is the most plesiomorphic taxon (following Krishtalka and Stucky, 1983a) such that *Peratherium* is the sister taxon to *Peradectes*; B) Given the character states observed within *Protalphadon* (Cifelli, 1990a), *Peradectes chesteri* is the most plesiomorphic taxon within *Peradectes*.


Peradectes
Alphadon
Protalphadon
Peratherium
P. elegans
P. minutus
P. chesteri
1', 2', 3'
1, 2, 3
1
1', 2', 3'
2, 3

character states:
- 1- paracone and metacone subequal; 1'- paracone shorter than metacone
- 2- protocone anteroposteriorly compressed; 2'- protocone longer or expanded
- 3-stylar cusps reduced to absent ; 3'- stylar cusps and conules stronger or larger

A

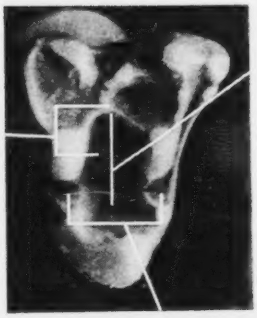

Peradectes
Peratherium
Alphadon
Protalphadon
P. chesteri
P. minutus
P. elegans
1', 2', 3'
1', 2', 3'
1, 2, 3

character states:
- 1- ratio of upper molar transverse width/ anteroposterior length high; 1'- ratio lower
- 2- protocone anteroposteriorly compressed; 2'- protocone longer or expanded
- 3- stylar cusps and conules stronger or larger; 3'- stylar cusps reduced to absent

character states 1, 2, 3 are found in the outgroup *Protalphadon*, and considered to be plesiomorphic for *Peradectes*.

B

Figure 14. Upper photograph- UALVP 22694, RM3 of *Alphadon jasoni* (Frenchman Formation), showing measurements used to characterize dilambdodont upper molars, including length, width and depth of the valley between the paracone and metacone. Lower photographs- stereopair of UALVP 22694.

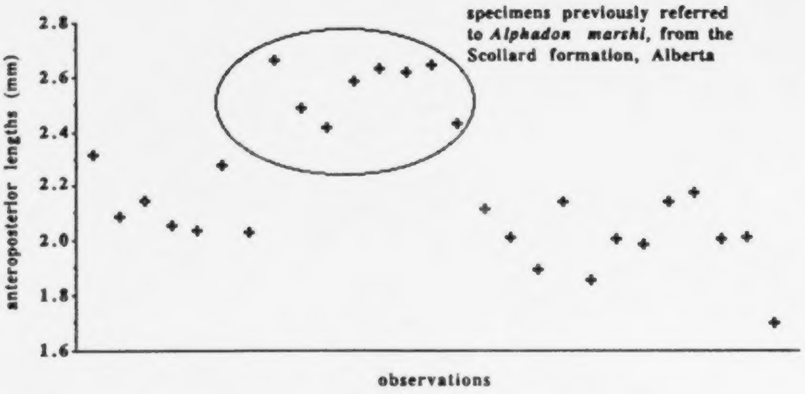


WIDTH: valley between paracone and metacone can be transversely NARROWER OR WIDER

DEPTH: valley may be SHALLOWER or DEEPER

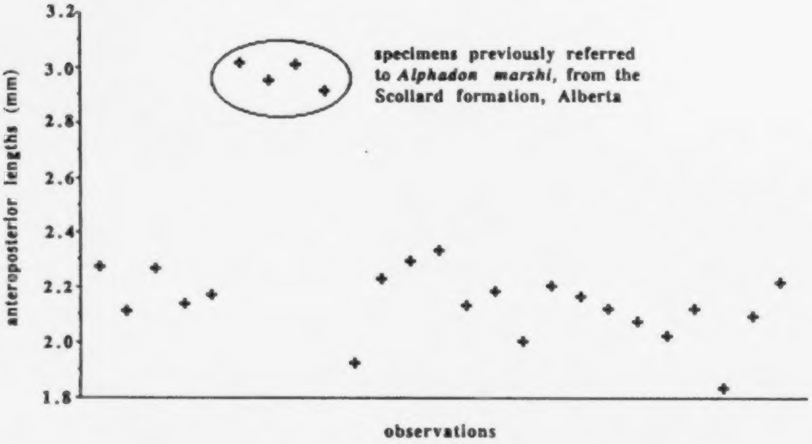
LENGTH: valley may be anteroposteriorly SHORTER or LONGER

Figure 15. Scattergrams showing the distribution of measurements (anteroposterior length) of A) M1s, B) M2s and C) M3s referred to *Alphadon jasoni*. The Y axis in these scattergrams represents anteroposterior length, while the X axis represents the tooth positions measured (first, second, third, etc.). Upper molar specimens referred to *A. jasoni* from the Scollard Formation, Alberta, are circled.



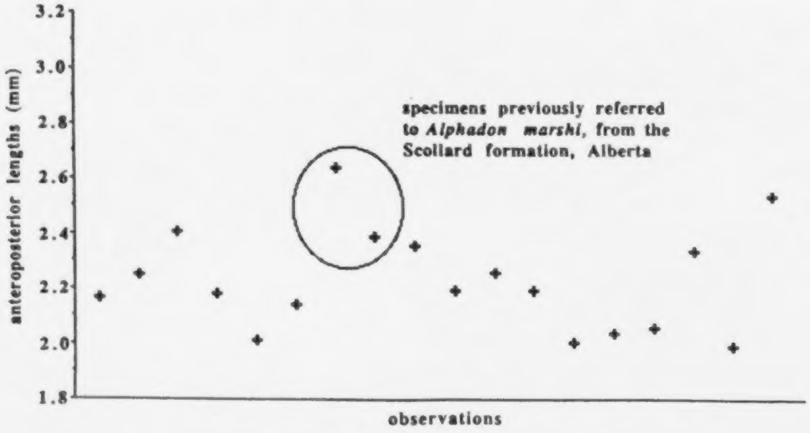
A

Scattergram: anteroposterior lengths of M1s referred to *Alphadon jasoni*



B

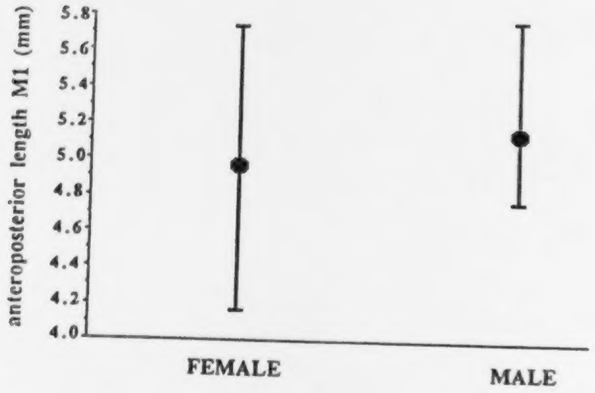
Scattergram: anteroposterior lengths of M2s referred to *Alphadon jasoni*



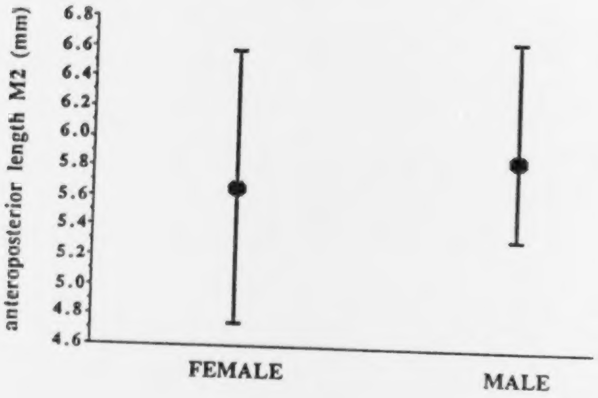
C

Scattergram: anteroposterior lengths of M3s referred to *Alphadon jasoni*

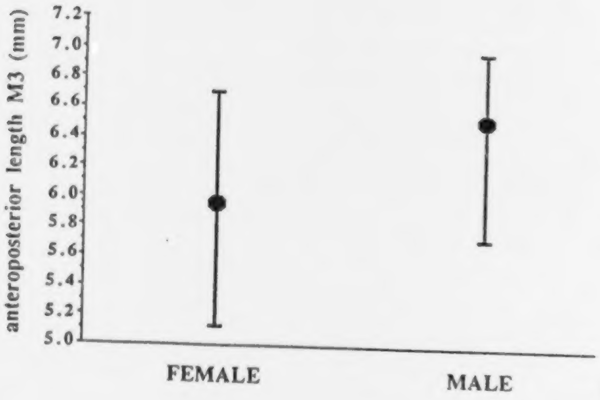
Figure 16. Ranges of anteroposterior length measurements for A) M1s, B) M2s, and C) M3s of *Didelphis virginiana*. Ranges are given for measurements taken from female and male indidividuals. The mean of the measurements for the females and males is given by the large circle.


anteroposterior length M1 (mm)
5.8
5.6
5.4
5.2
5.0
4.8
4.6
4.4
4.2
4.0
FEMALE
MALE

A

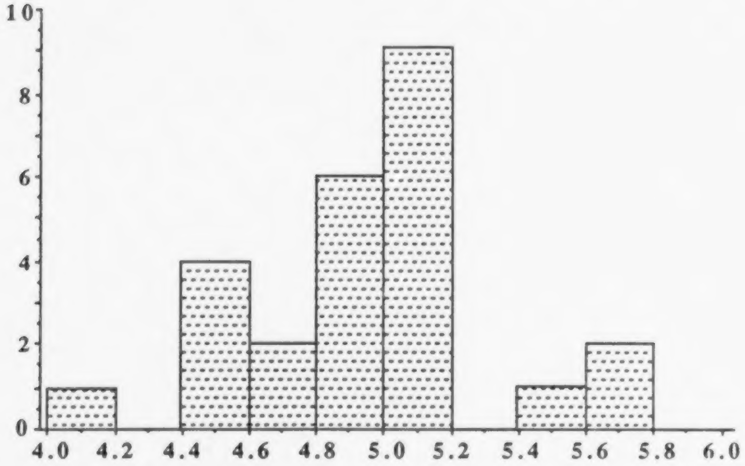

anteroposterior length M2 (mm)
6.8
6.6
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
FEMALE
MALE

B

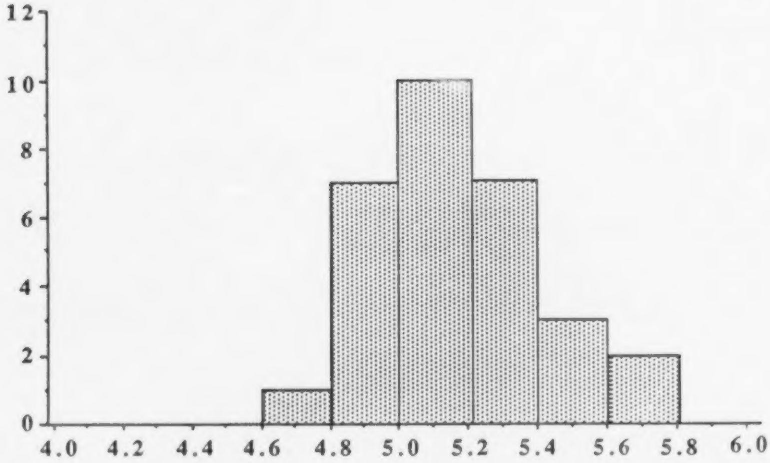

anteroposterior length M3 (mm)
7.2
7.0
6.8
6.6
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
FEMALE
MALE

C

Figure 17. Histograms showing the distribution of measurements of M1s of *Didelphis virginiana*. The X axis shows the intervals of measurement (in mm.), and the Y axis indicates the number of measurements per interval; A) Distribution of measurements from female individuals; B) Distribution of measurements from male individuals.

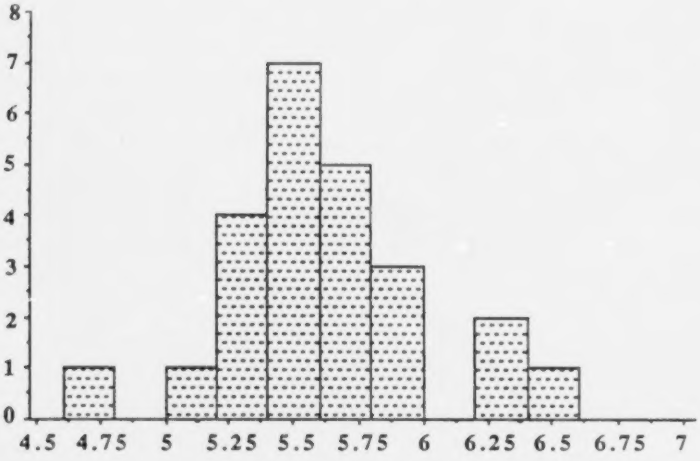

10
8
6
4
2
0
4.0
4.2
4.4
4.6
4.8
5.0
5.2
5.4
5.6
5.8
6.0

A

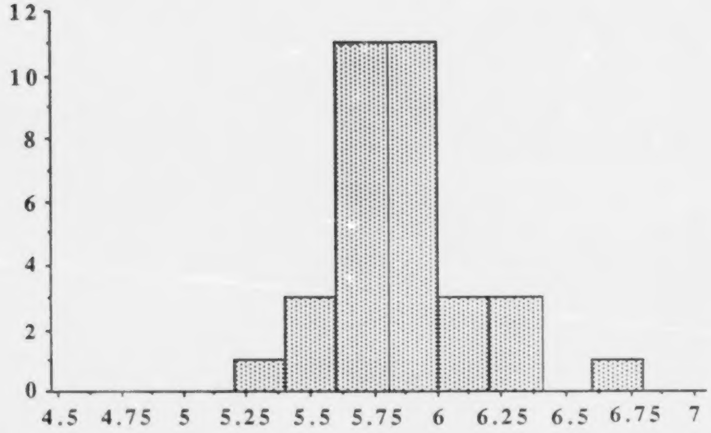

12
10
8
6
4
2
0
4.0
4.2
4.4
4.6
4.8
5.0
5.2
5.4
5.6
5.8
6.0

B

Figure 18. Histograms showing the distribution of measurements of M2s of *Didelphis virginiana*. The X axis shows the intervals of measurement (in mm.), and the Y axis indicates the number of measurements per interval; A) Distribution of measurements from female individuals; B) Distribution of measurements from male individuals.

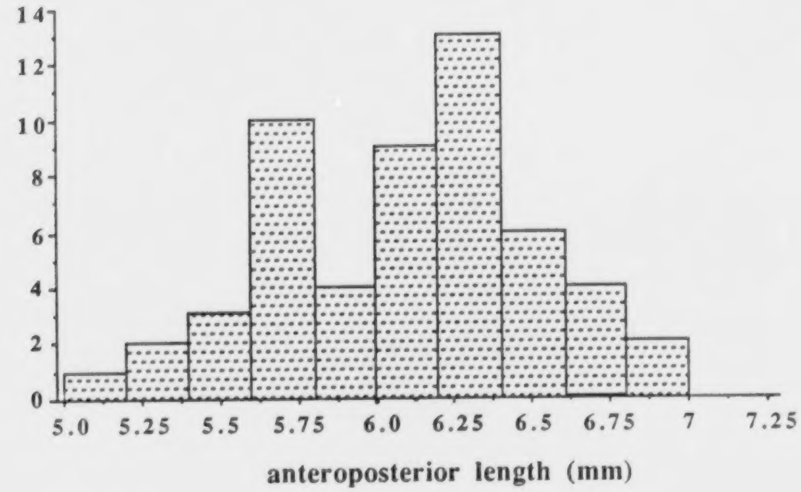

8
7
6
5
4
3
2
1
0
4.5
4.75
5
5.25
5.5
5.75
6
6.25
6.5
6.75
7

A

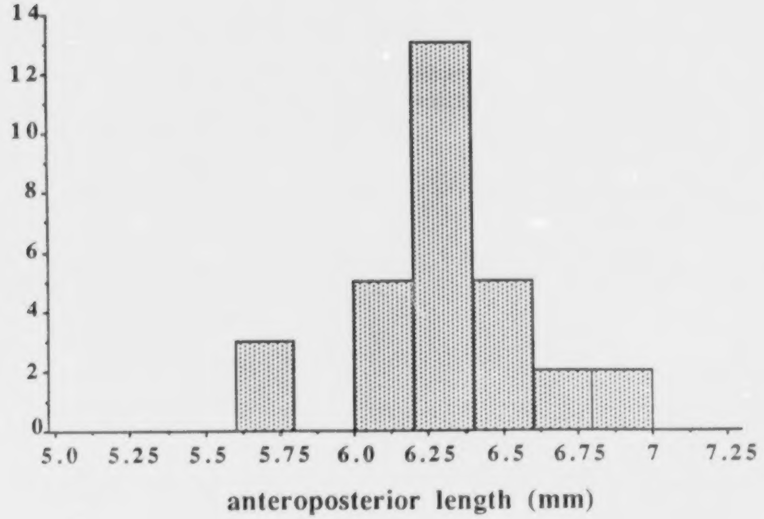

12
10
8
6
4
2
0
4.5
4.75
5
5.25
5.5
5.75
6
6.25
6.5
6.75
7

B

Figure 19. Histograms showing the distribution of measurements of M3s of *Didelphis virginiana*. The X axis shows the intervals of measurement (in mm.), and the Y axis indicates the number of measurements per interval; A) Distribution of measurements from female individuals; B) Distribution of measurements from male individuals.

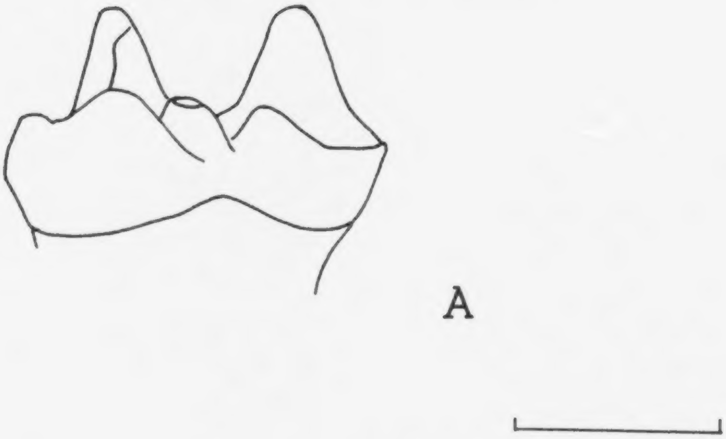

14
12
10
8
6
4
2
0
5.0
5.25
5.5
5.75
6.0
6.25
6.5
6.75
7
7.25
anteroposterior length (mm)

A

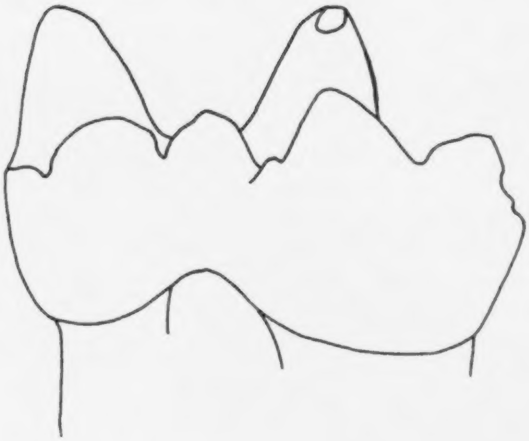

14
12
10
8
6
4
2
0
5.0
5.25
5.5
5.75
6.0
6.25
6.5
6.75
7
7.25
anteroposterior length (mm)

B

Figure 20. Camera lucida drawings of upper molar specimens referred to *Alphadon jasoni*, showing the relative heights of the paracone and metacone. Labial views A) UALVP 3708 M3, *Alphadon jasoni*; B) M3 of UALVP 2846, *Alphadon jasoni*. Scale =1mm.



A



B

Figure 21. Strict consensus tree of 113 minimal length trees (length 107, C. I., . 561, produced by the heuristics methodology (PAUP 3.0) from the data set of unordered and unweighted characters (43 characters, 21 taxa).

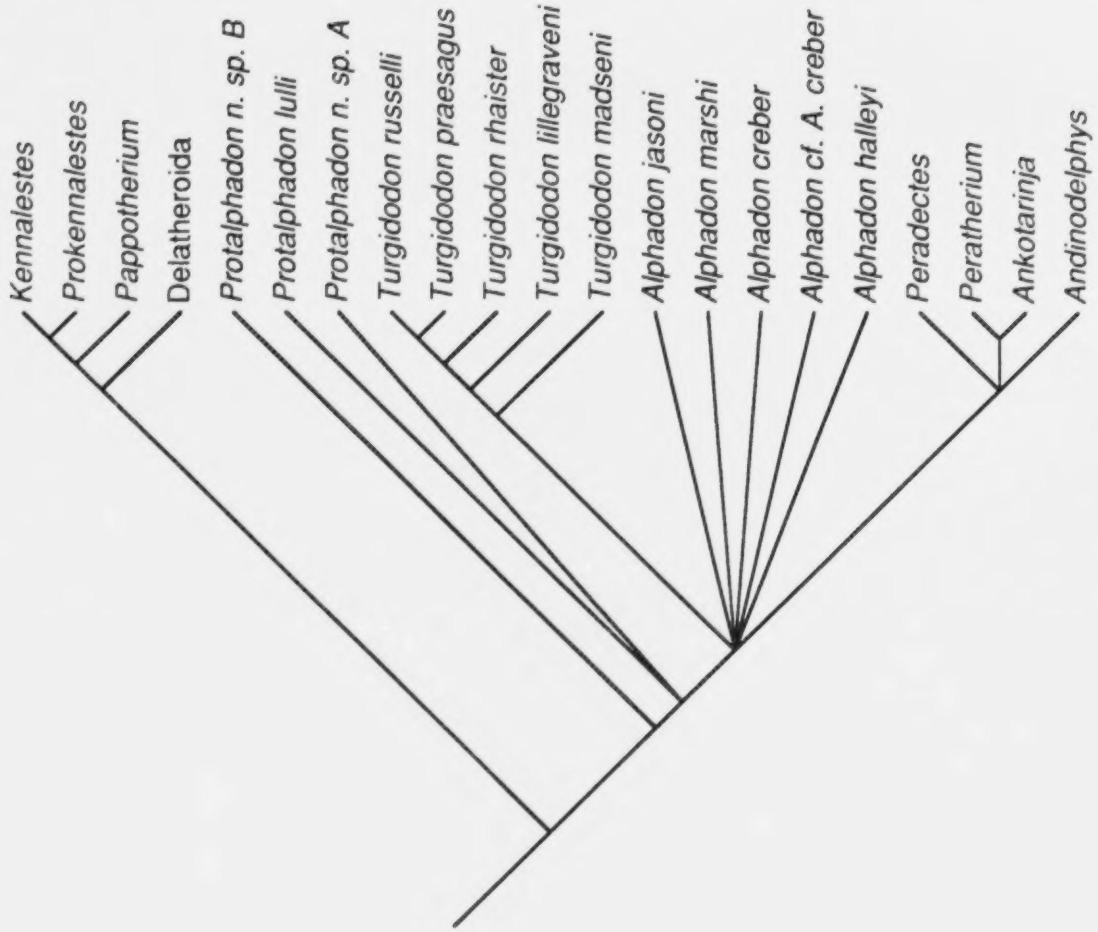

Kennalestes
Prokennalestes
Pappotherium
Deltatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon jasoni
Alphadon marshi
Alphadon creber
Alphadon cf. A. creber
Alphadon halleyi
Peradectes
Peratherium
Ankotarinja
Andinodelphys

Figure 22. Strict consensus tree of 34 minimal length trees (length 617, C. I., .669) produced by the heuristics methodology (PAUP 3.0) from the data set in which characters were unordered but reweighted using the successive approximations method of Farris (1969).

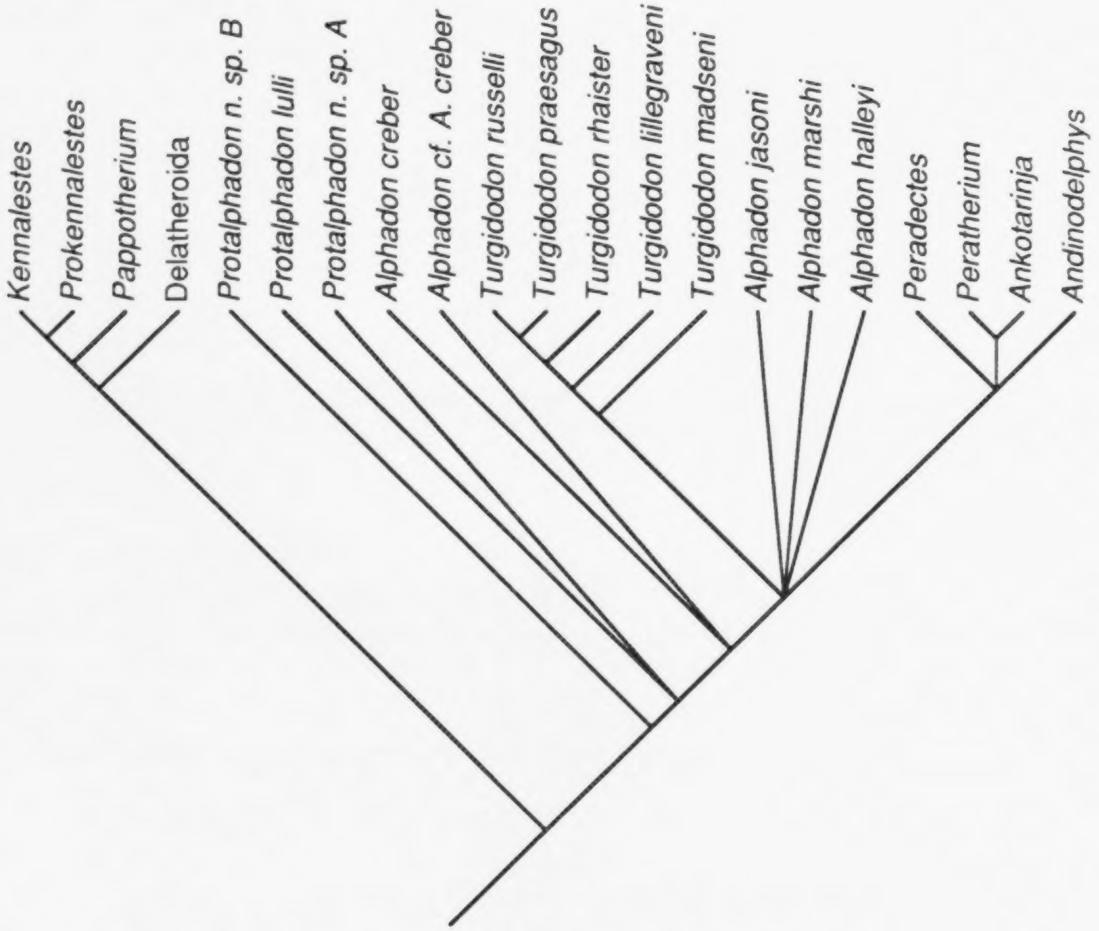

Kennalestes
Prokennalestes
Pappotherium
Deltatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Alphadon creber
Alphadon cf. A. creber
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon jasoni
Alphadon marshi
Alphadon halleyi
Peradectes
Peratherium
Ankotarinja
Andinodelphys

Figure 23. Strict consensus tree of 141 minimal length trees (length 107, C. I., . 561), produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters unweighted.

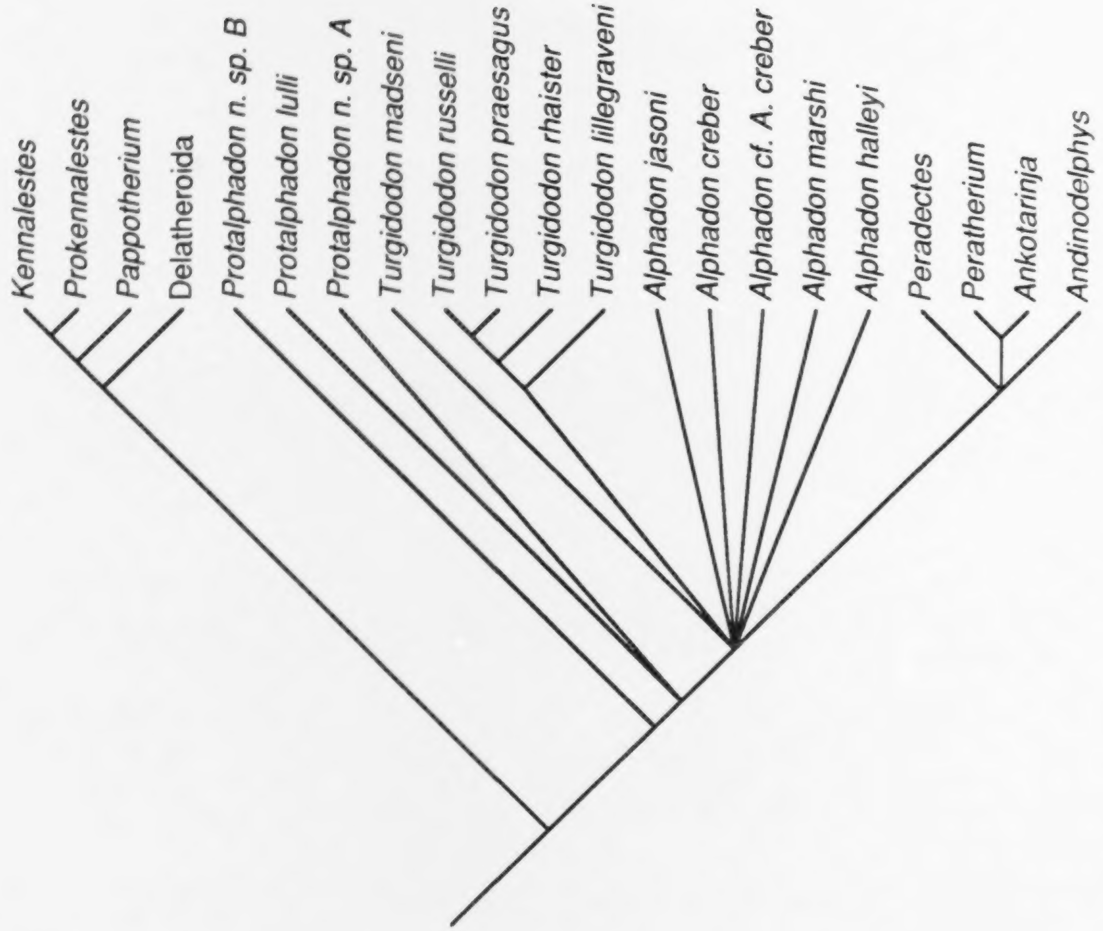

Kennalestes
Prokennalestes
Pappotherium
Deltatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Turgidodon madseni
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Alphadon jasoni
Alphadon creber
Alphadon cf. A. creber
Alphadon marshi
Alphadon halleyi
Peradectes
Peratherium
Ankotarinja
Andinodelphys

Figure 24. Semistrict consensus tree of 141 minimal length trees (length 107, C. I., .561), produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters unweighted.

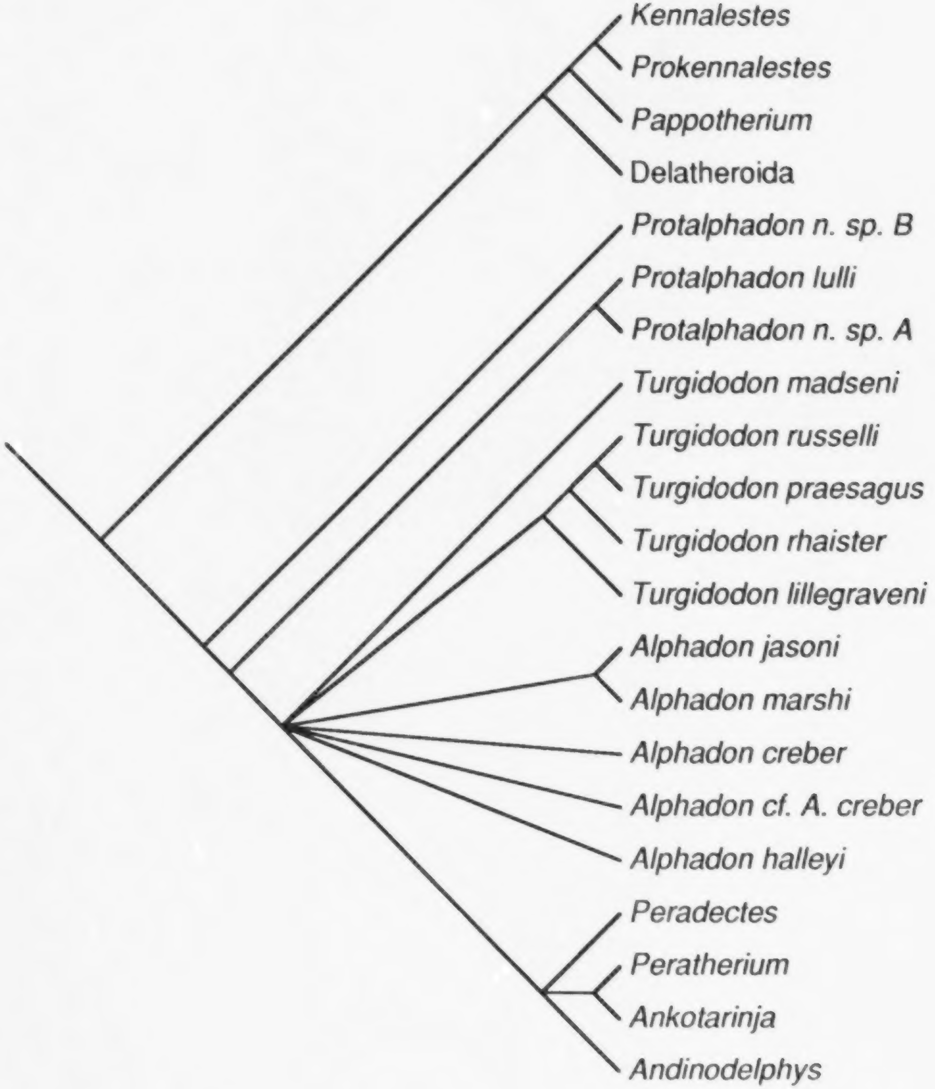

Kennalestes
Prokennalestes
Pappotherium
Delatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Turgidodon madseni
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Alphadon jasoni
Alphadon marshi
Alphadon creber
Alphadon cf. A. creber
Alphadon halleyi
Peradectes
Peratherium
Ankotarinja
Andinodelphys

Figure 25. Strict consensus tree of 36 minimal length trees (length 638, C. I., .663), produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters reweighted (Farris, 1969).

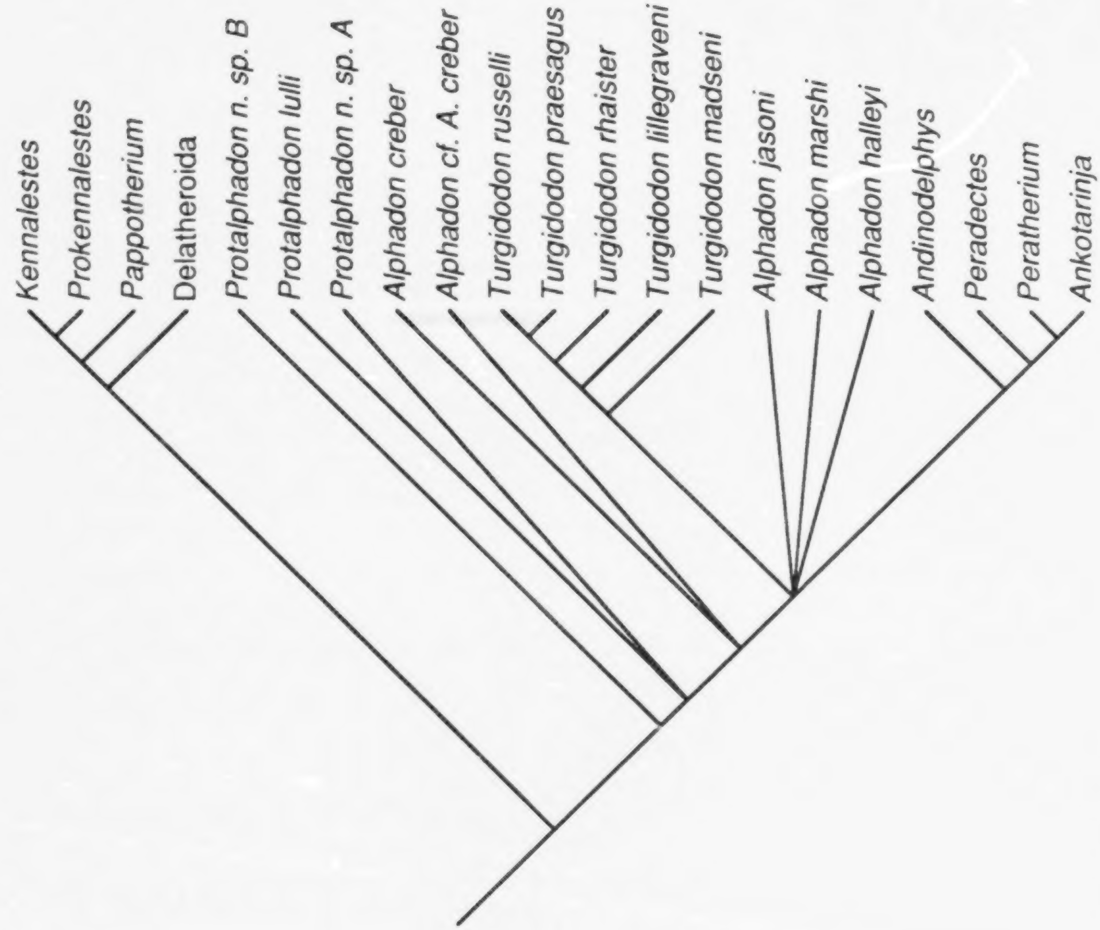

Kennalestes
Prokennalestes
Pappotherium
Delatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Alphadon creber
Alphadon cf. A. creber
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon jasoni
Alphadon marshi
Alphadon halleyi
Andinodelphys
Peradectes
Peratherium
Ankotarinja

Figure 26. Semistrict consensus tree of 36 minimal length trees (length 638, C. I., .663), produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters reweighted (Farris, 1969).

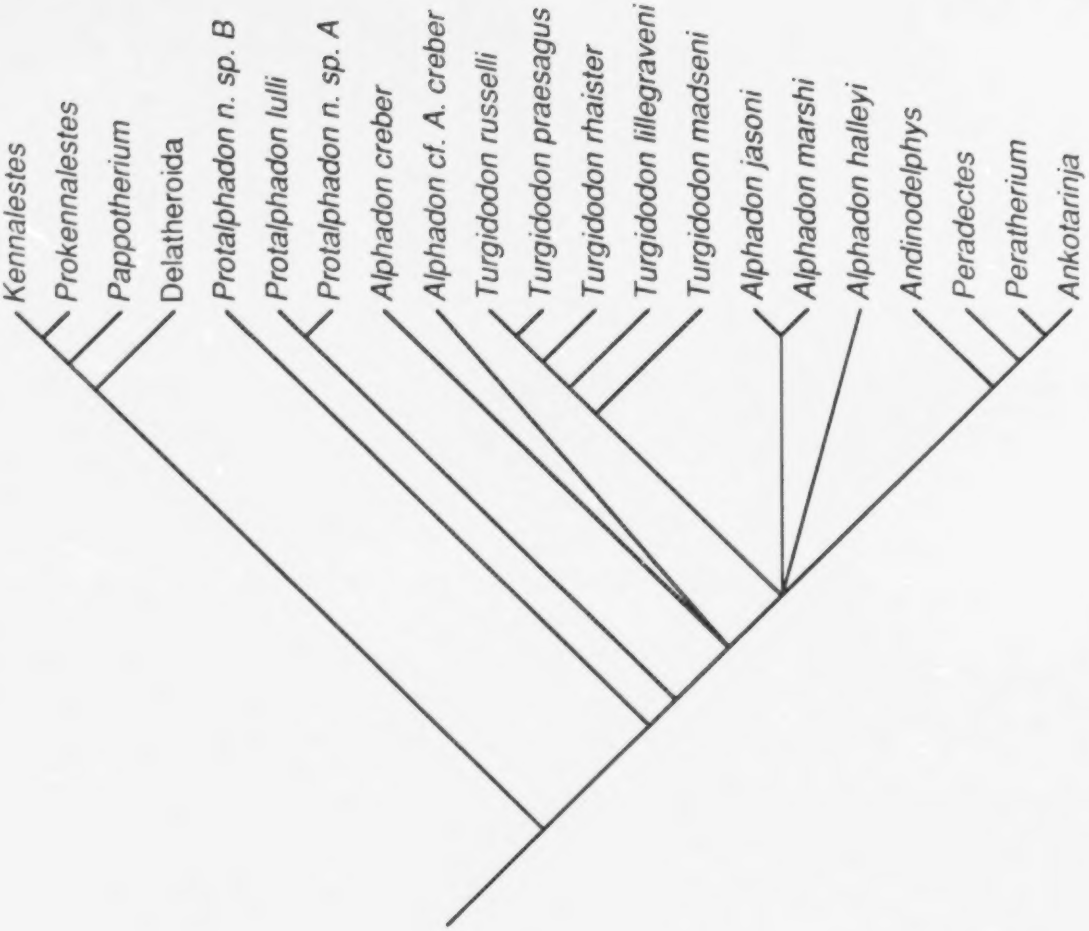

Kennalestes
Prokennalestes
Pappotherium
Delatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Alphadon creber
Alphadon cf. A. creber
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon jasoni
Alphadon marshi
Alphadon halleyi
Andinodelphys
Peradectes
Peratherium
Ankotarinja

Figure 27. Adams consensus tree of 36 minimal length trees (length 638, C. I., .663), produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters reweighted (Farris, 1969).

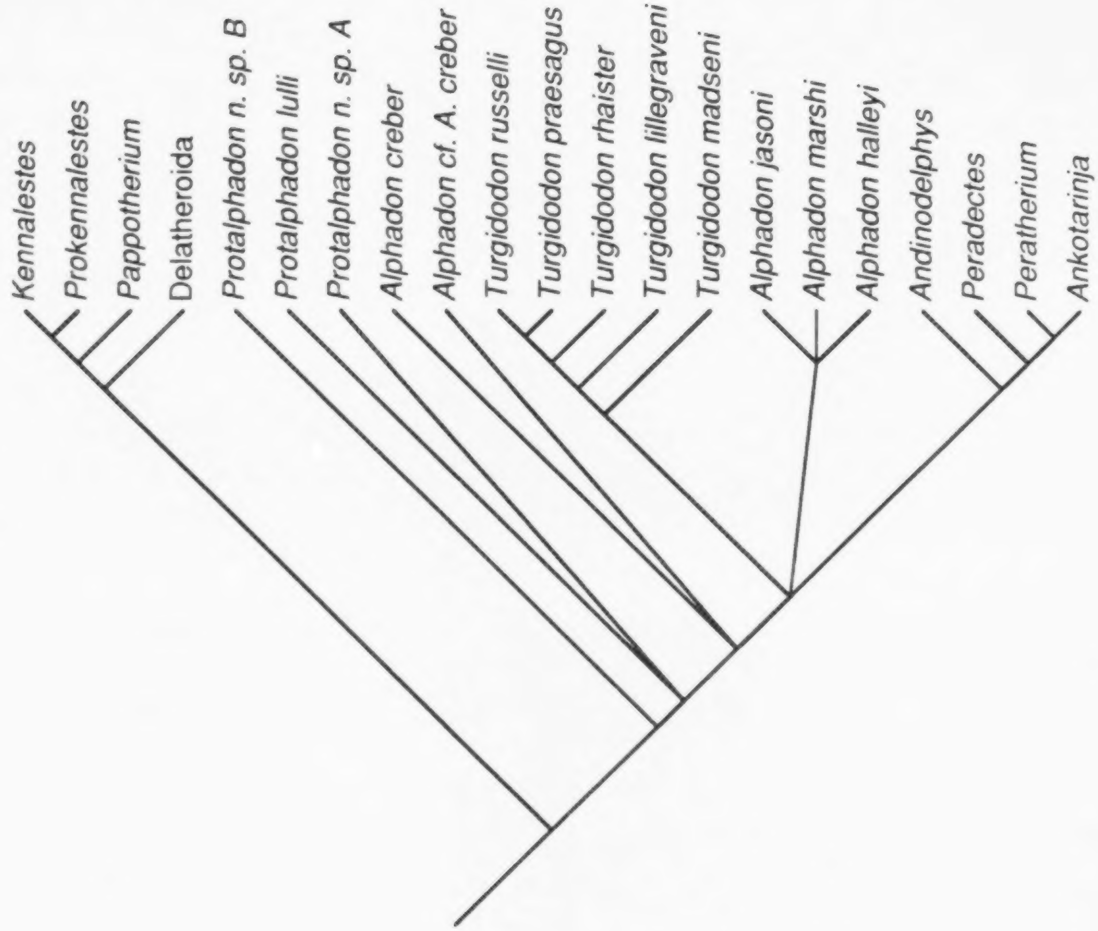
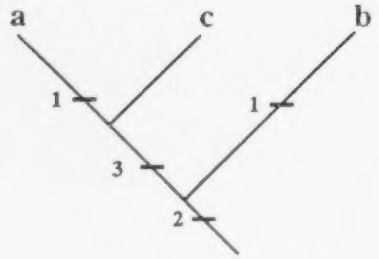
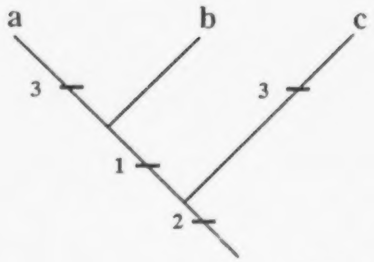

Kennalestes
Prokennalestes
Pappotherium
Delatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Alphadon creber
Alphadon cf. A. creber
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon jasoni
Alphadon marshi
Alphadon halleyi
Andinodelphys
Peradectes
Peratherium
Ankotarinja

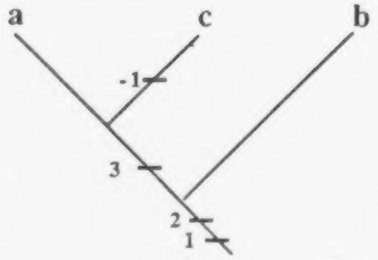
Figure 28. Minimal length cladograms (A1, 2; B1, 2) and the resulting strict consensus cladogram (C, D). In cladogram A1, 2, taxa **a** and **c** are grouped by a synapomorphy for character 3, while in cladogram B1, 2, taxa **a** and **b** are grouped by a synapomorphy for character 1. C, D) When a strict consensus cladogram of A1 and B1 (or A2, B2) is produced, these three taxa are placed in a polytomy, and there is one extra step involved (five in cladograms C and D vs. four in A and B) because reversals (C) or convergences (D) in characters 1 and 3 occur simultaneously.



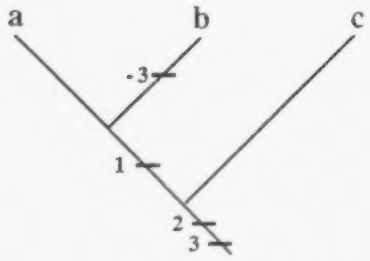
A1



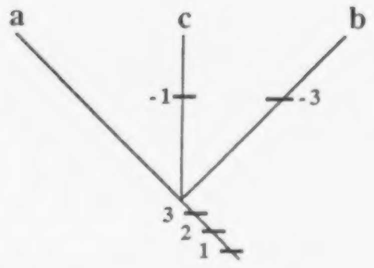
A2



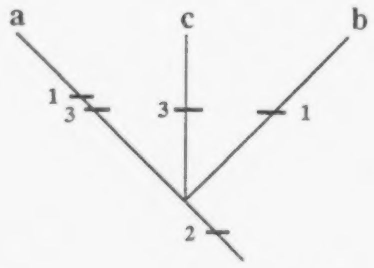
B1



B2



C



D

Figure 29. Original cladogram number 22 (of 36 original minimal length cladograms produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters reweighted), chosen to examine the distributions of character states, as outlined in Chapter 4.

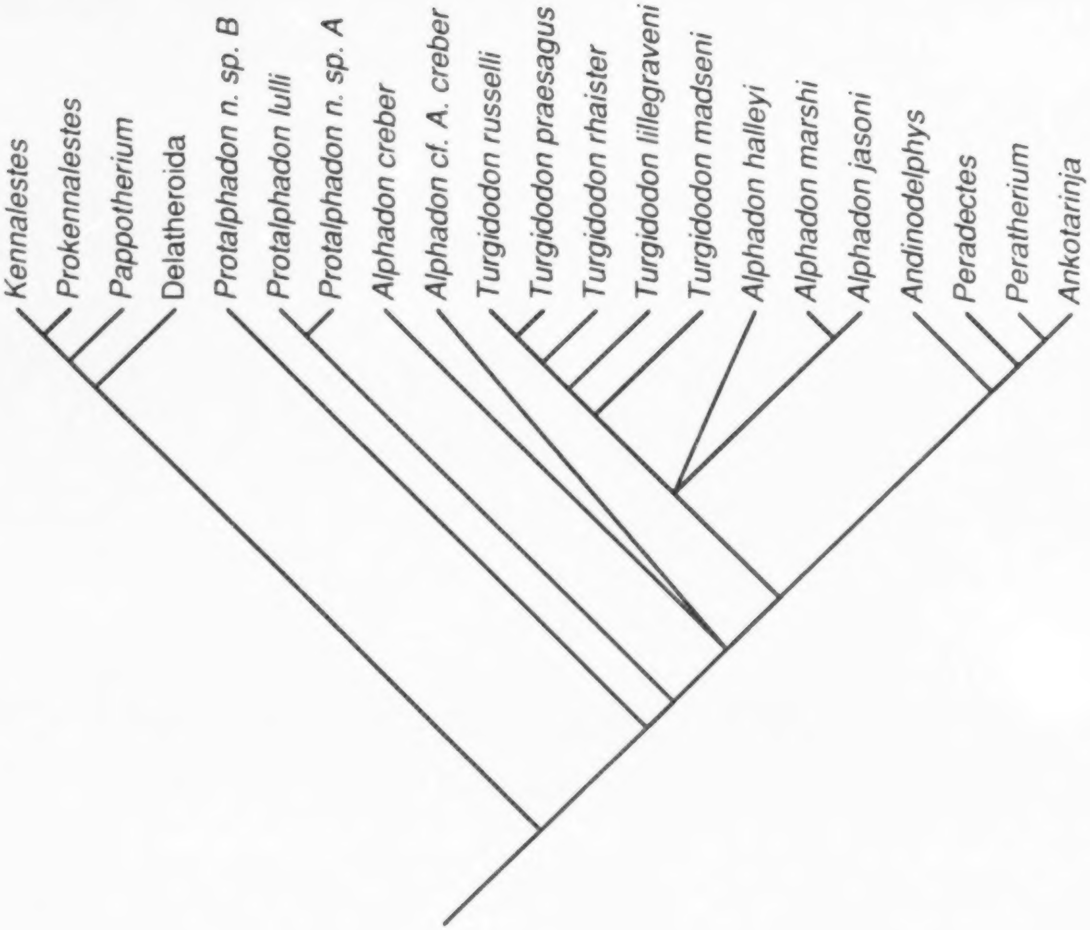
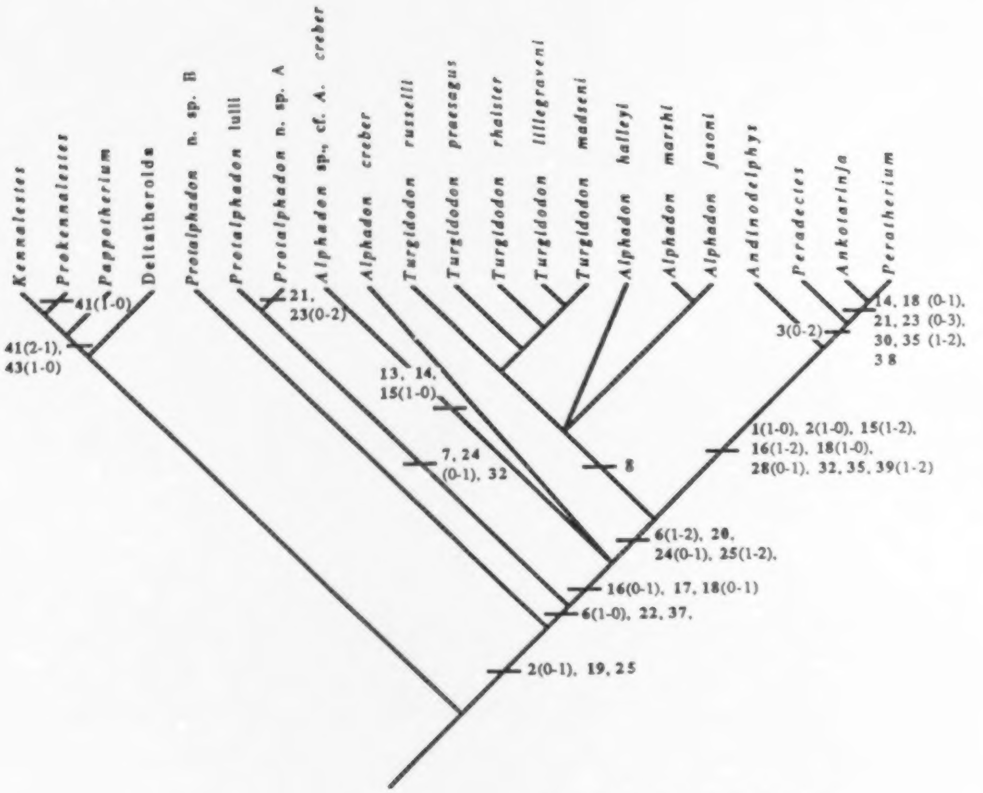
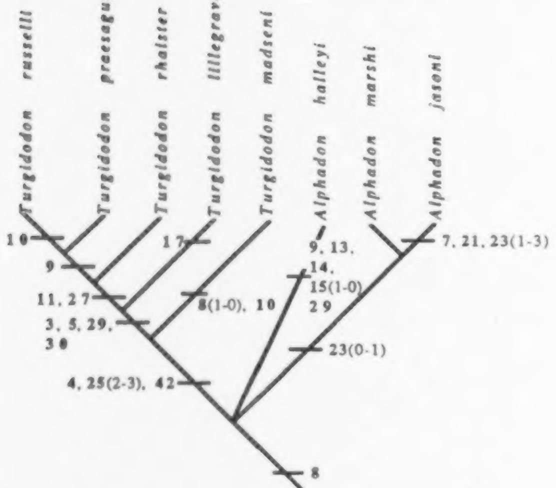

Kennalestes
Prokennalestes
Pappotherium
Delatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Alphadon creber
Alphadon cf. A. creber
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon halleyi
Alphadon marshi
Alphadon jasoni
Andinodelphys
Peradectes
Peratherium
Ankotarinja

Figure 30. The distribution of character states (synapomorphies), as taken from (and mapped onto) original cladogram number 22. A) for all taxa except *Turgidodon* and *Alphadon* s.s.*, B) for *Turgidodon* and *Alphadon* s.s.*


Kennalestes
Prokennalestes
Pappotherium
Deltatheroida
Protalphadon n. sp. B
Protalphadon lulli
Protalphadon n. sp. A
Alphadon sp., cf. A. creber
Alphadon creber
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon halleyi
Alphadon marshi
Alphadon jasoni
Andinodelphys
Peradectes
Ankotarinja
Peratherium
41(1-0)
41(2-1), 43(1-0)
21, 23(0-2)
13, 14, 15(1-0)
7, 24 (0-1), 32
8
14, 18 (0-1), 21, 23 (0-3), 30, 35 (1-2), 3 8
3(0-2)
1(1-0), 2(1-0), 15(1-2), 16(1-2), 18(1-0), 28(0-1), 32, 35, 39(1-2)
6(1-2), 20, 24(0-1), 25(1-2),
16(0-1), 17, 18(0-1)
6(1-0), 22, 37,
2(0-1), 19, 25

where no state changes are given, character transformations are 0-1

A


Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon halleyi
Alphadon marshi
Alphadon jasoni
1 0
9
11, 2 7
3, 5, 29, 3 0
1 7
8(1-0), 10
9, 13, 14, 15(1-0) 2 9
7, 21, 23(1-3)
23(0-1)
4, 25(2-3), 42
8

B

Figure 31. New taxa erected in this analysis, and used in the final classification, as described in Chapter 5.

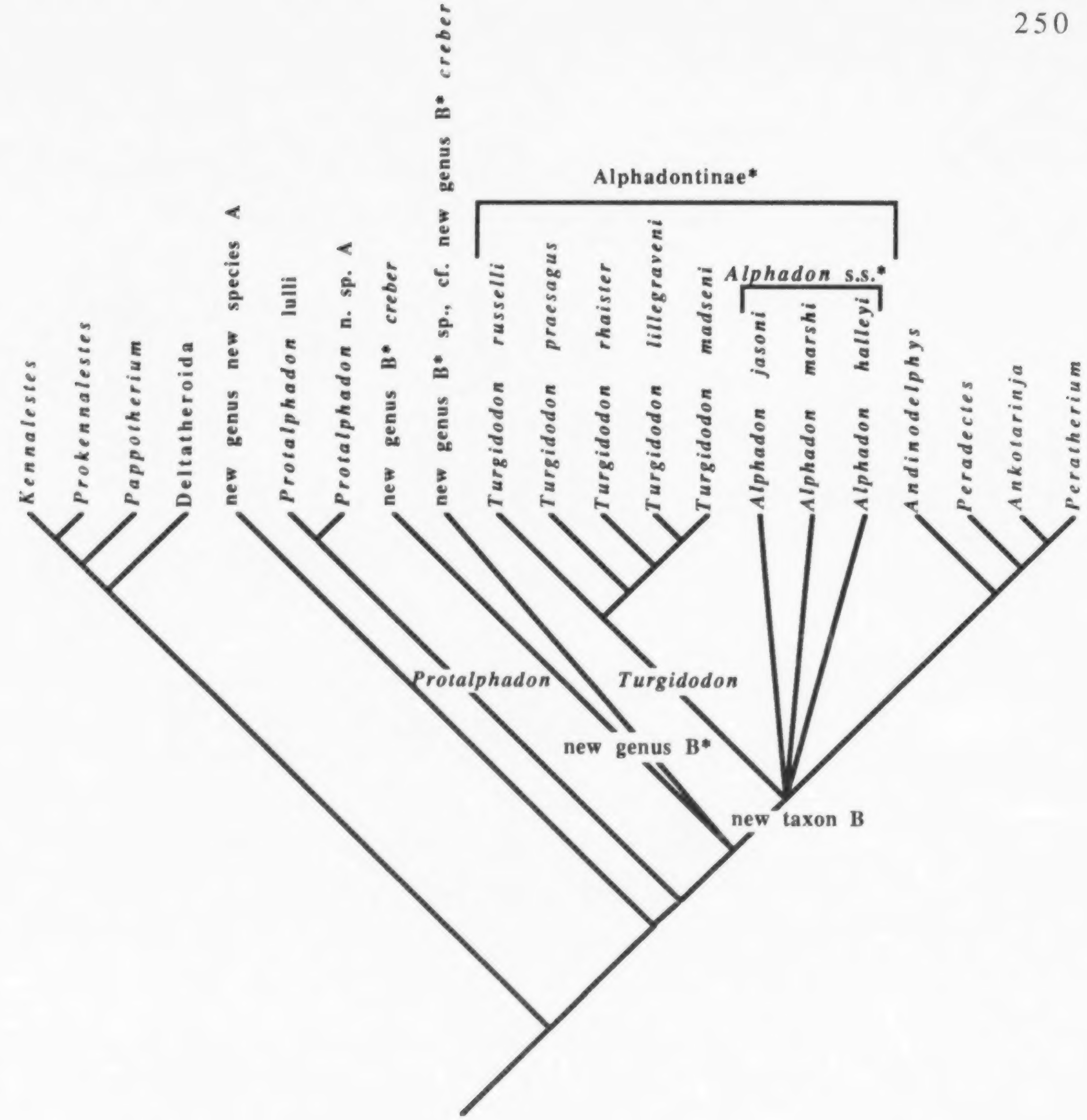
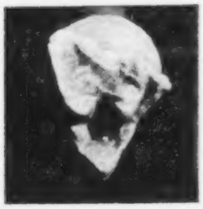
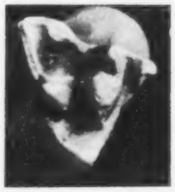
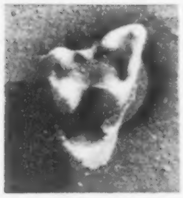

Kennalestes
Prokennalestes
Pappotherium
Deltatheroida
new genus new species A
Protalphadon lulli
Protalphadon n. sp. A
new genus B* *creber*
new genus B* sp., cf. new genus B* *creber*
Alphadontinae*
Turgidodon russelli
Turgidodon praesagus
Turgidodon rhaister
Turgidodon lillegraveni
Turgidodon madseni
Alphadon s.s.*
Alphadon jasoni
Alphadon marshi
Alphadon halleyi
Andinodelphys
Peradectes
Ankotarinja
Peratherium
Protalphadon
Turgidodon
new genus B*
new taxon B

Plate 1. *Alphadon* sp., cf. *A. creber*, Milk River Formation, Alberta, Wahweap Formation, Utah. Specimens with UALVP 55-- numbers originally referred to *Alphadon creber* byFox (1971), OMNH 20968, originally referred to *Anchistodelphys archibaldi* Cifelli, 1990a, OMNH 20115, formerly the holotype of *Protalphadon wahweapensis* Cifelli, 1990a. A) UALVP 5551, RM1; B) UALVP 29517, RM1; C) OMNH 20968, LM1; D) UALVP 5558, RM1, labial fragment; E) UALVP 5553, holotype of *Alphadon* sp., cf. *A. creber*, LM1; F) UALVP 5585, RM1; G) UALVP 29593, LM1; H) UALVP 29520, RM1; I) UALVP 5541, RM2; J) UALVP 22626, RM2; K) UALVP 29630, LM2; L) OMNH 20115, LM2; M) UALVP 5545, LM3. All x11.


A


B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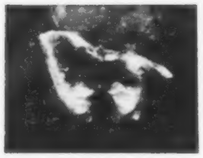
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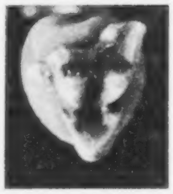
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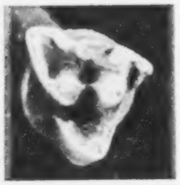
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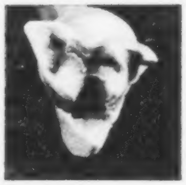
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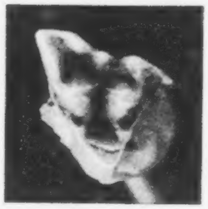
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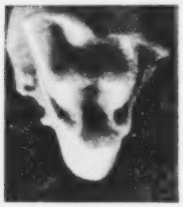
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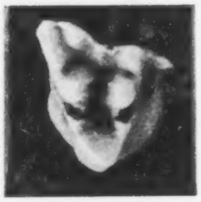
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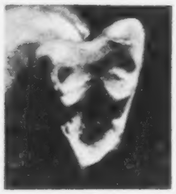
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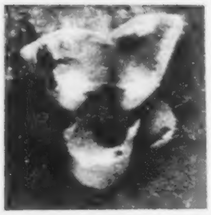
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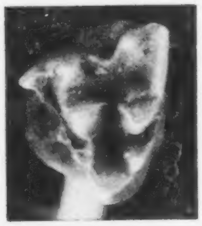
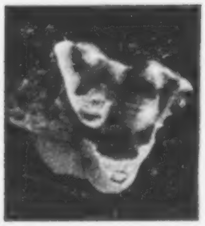

M

Plate 2. *Alphadon creber*, Milk River Formation, Alberta. OMNH 20587 originally assigned to *Protoalphadon wahweapensis* Cifelli, 1990a. A) UALVP 29519, RM1; B) UALVP 29521, RM1; C) OMNH 20587, LM1, originally assigned to *Protoalphadon wahweapensis*; D) UALVP 29533, LM2; E) UALVP 5545, holotype of *A. creber*, partial right maxillary fragment preserving M3 and the alveoli of M4; F) UALVP 5557, LM3; G) UALVP 29525, RM3; H) UALVP 5542, LM3. All x11.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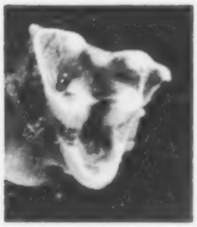
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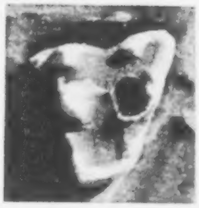
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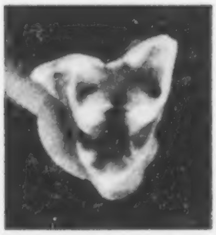
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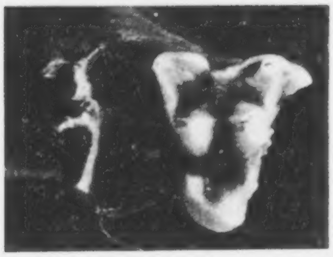
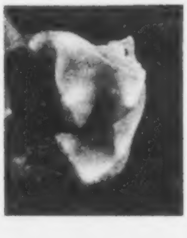

E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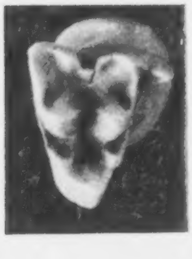
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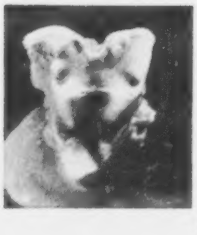
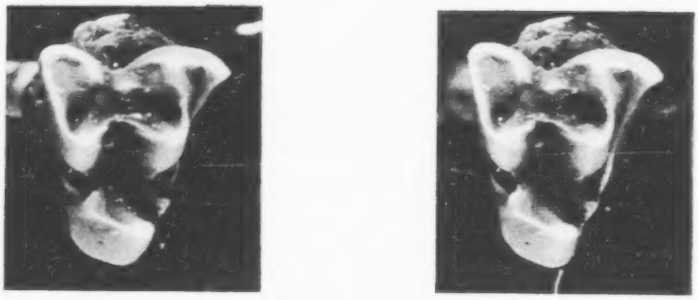
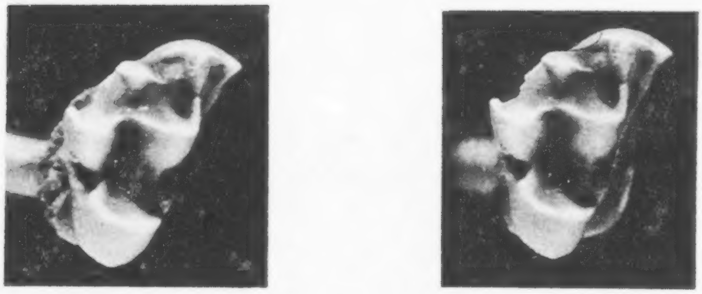

H

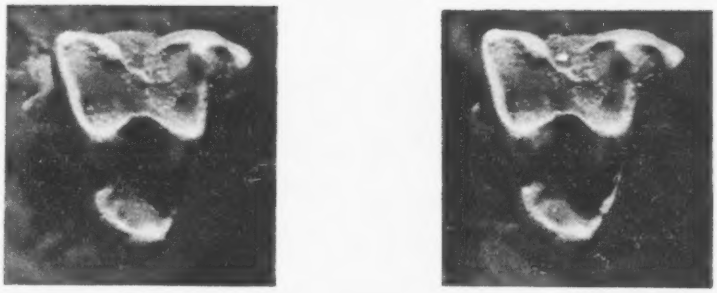
Plate 3. *Protalphadon* n. sp. A., Hell Creek Formation, Montana. Stereopairs, A) UCMP 1117696, RM3; B) UCMP 117695, RM3; C) UCMP 109031, RM3, all previously classified as "*A.*" *lulli*. All x 15.



A



B



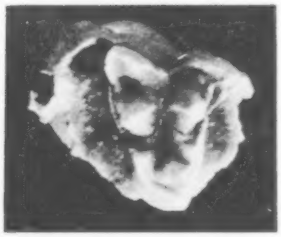
C

Plate 4. *Protalphadon* n. sp. B., Kaiparowits Formation, Utah. A) OMNH 20120, RM3; B) OMNH 20160, RM3. Previously classified as *Iqualadelphis lactea* by Cifelli (1990a), both x15.

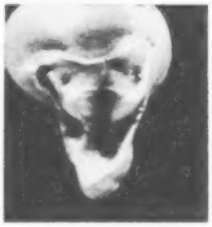
A

B

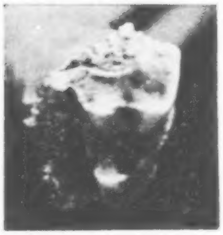
Plate 5. *Iqualadelphis lactea*, Milk River Formation, Alberta. A) uncatalogued specimen of "*Pediomys*" *prokrejcii*, RM3 (Oldman Formation, Alberta); B) UALVP 22823, holotype of *I. lactea*, LM3; C) UALVP 22827, LM3; D) UALVP 29676, newly referred specimen, left maxillary fragment preserving M3 and anterolabial portion of M4; E) UALVP 22828, possible M2. All approximately x12.



A



B



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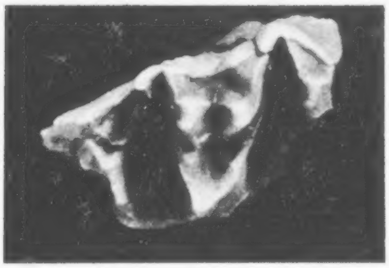

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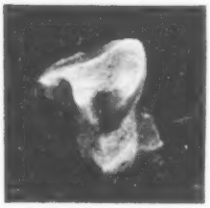
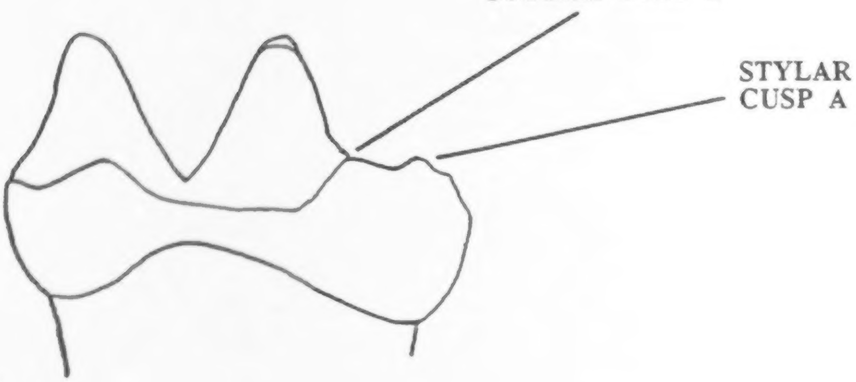
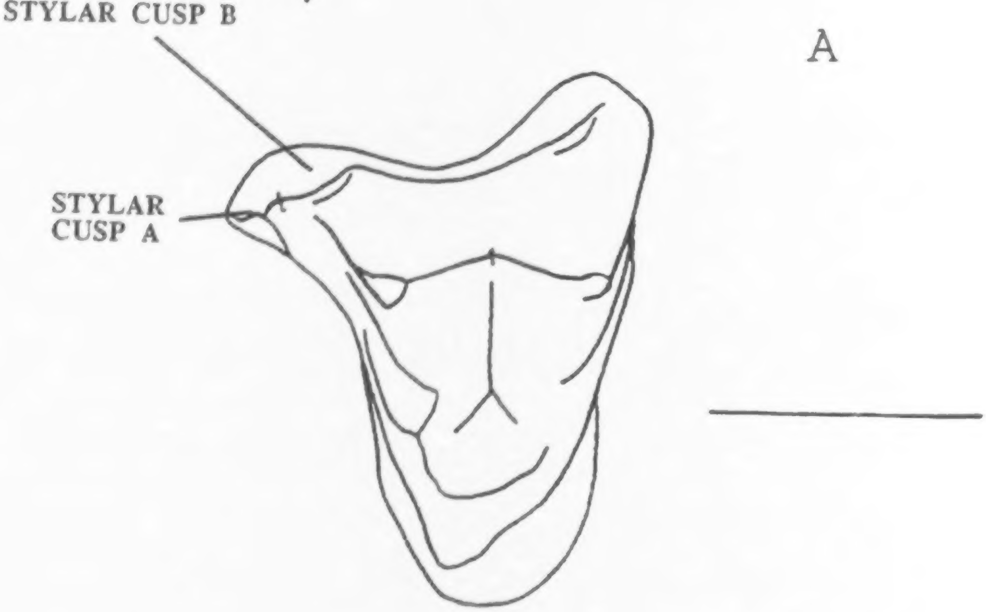


E

Plate 6. UALVP 22823, holotype of *Iqualadelphis lactea*. Camera lucida drawings of A) labial view showing relative sizes of stylar cusps A and B; B) occlusal view, scale = 1mm.

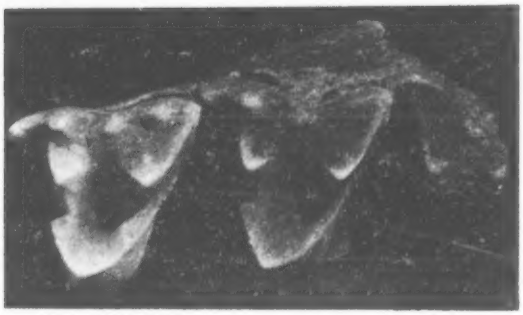

STYLAR CUSP B
STYLAR CUSP A

A


STYLAR CUSP B
STYLAR CUSP A

B

Plate 7. *Turgidodon russelli*, Oldman Formation, Alberta. A) UALVP 6957, maxillary fragment preserving M2-3; B) UALVP UCD, RM1, preserving labial half of tooth; C) UALVP 6952, LM1; D) UALVP 6956, LM1; E) UALVP 1486, RM1; F) UALVP 6953, LM1. All x11.



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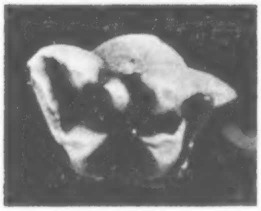

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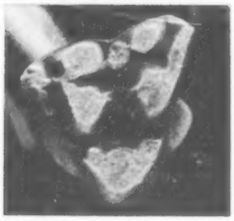

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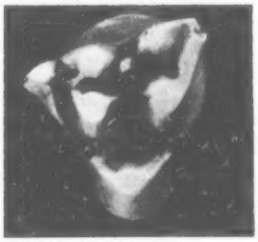

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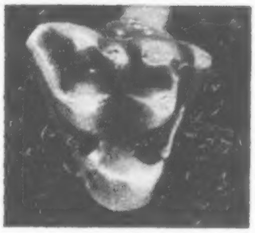

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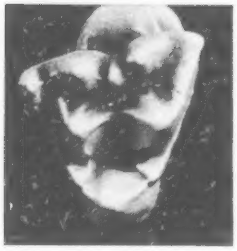
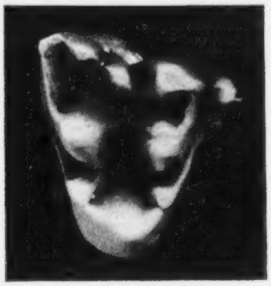


F

Plate 8. *Turgidodon russelli*, Oldman, Judith River formations. A) UALVP 6934, RM2; B) UALVP UCE, RM2; C) AMNH 109461, LM2 (Judith River Formation, Montana); D) UALVP UC9, RM3; E) UALVP 6983, RM3; F) UALVP UC12, RM3; G) UALVP 6939, RM3; H) UALVP UCH, LM3. All x11.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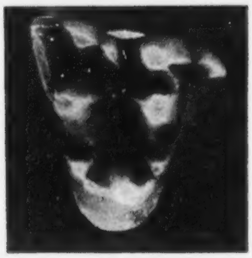
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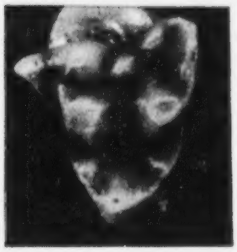
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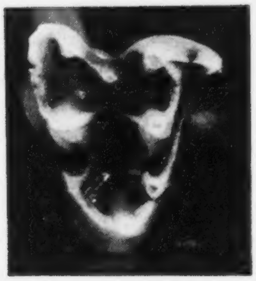
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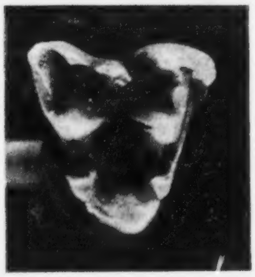
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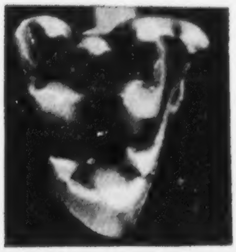
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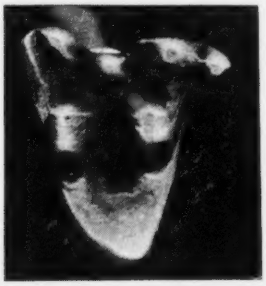
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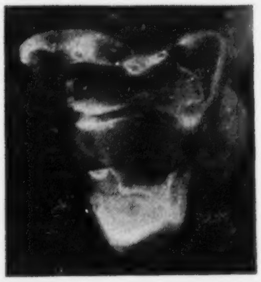
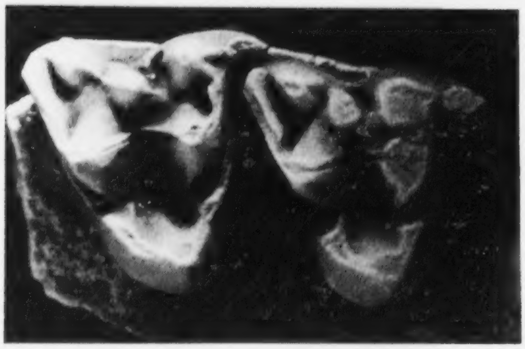

H

Plate 9. *Turgidodon praesagus*, Oldman Formation, Alberta. A) UALVP 1786, partial maxillary fragment preserving LM2-3; B) UALVP 6935, RM1; C) UALVP 6937, RM2; D) UALVP UC1, RM2; E) UALVP UC6, LM2; F) UALVP 4270, LM3; G) UALVP UC7, RM3. All x11.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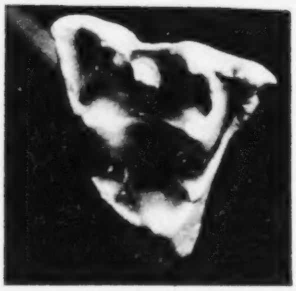
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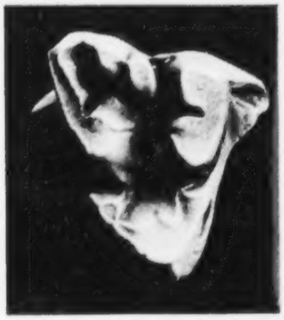
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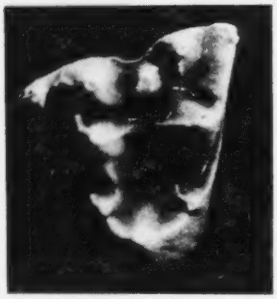
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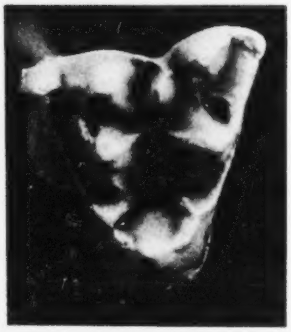
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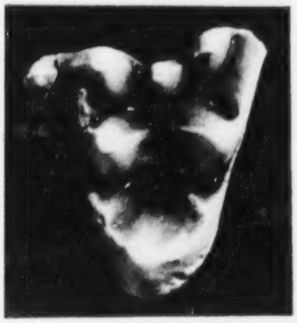
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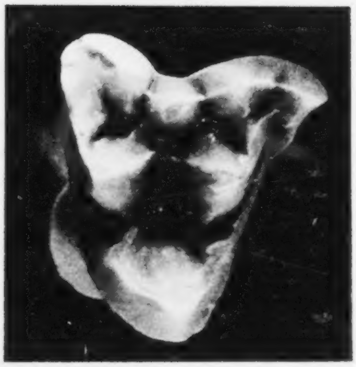
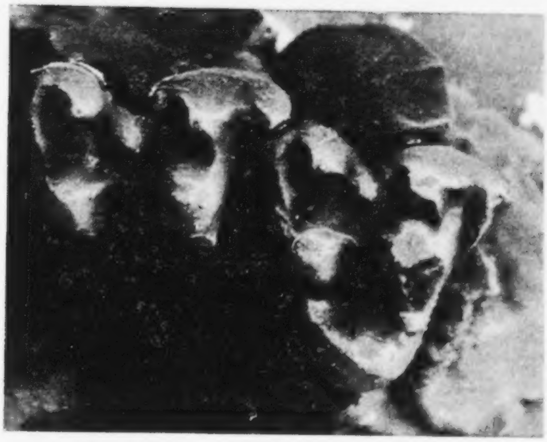

G

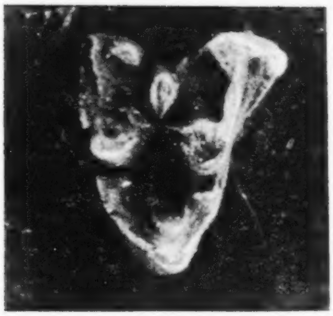
Plate 10. *Turgidodon lillegraveni*, Kaiparowits Formation, Utah. A) OMNH 20540, partial right maxillary fragment preserving M2-3; B) OMNH 20539, RM3. All x13.



A

B

Plate 11. Comparison of the holotypes of *Alphadon marshi* and "*Alphadon wilsoni*". A) YPM 13659, type specimen of *Alphadon marshi*, RM3, Lance Formation, Wyoming; B) UALVP 3146, type specimen of "*Alphadon wilsoni*", partial right maxillary fragment preserving M2-3, Scollard Formation, Alberta. Both x13.



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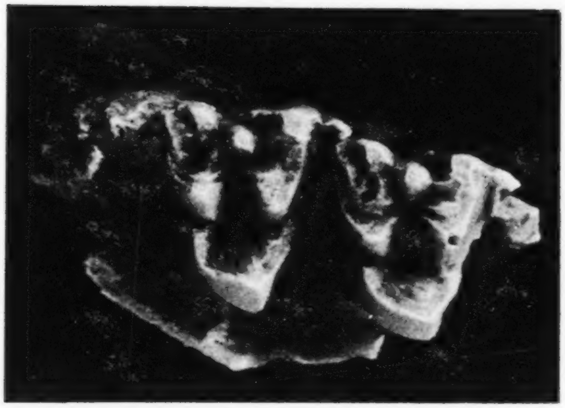
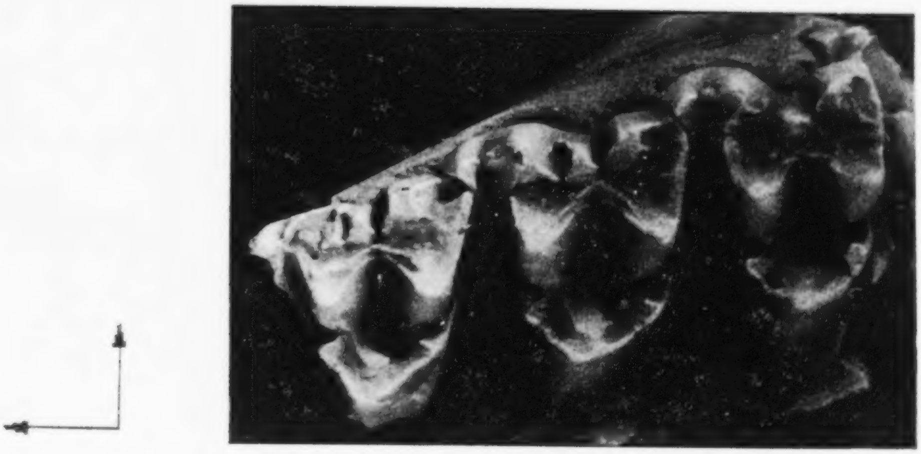


B

Plate 12. UALVP 2846, Scollard Formation, Alberta. Includes upper (M1-4) and lower molars (p3-m4) found in occlusion. A) LM1-3; M4 not included in figure; B) talonid of Lm1 and m2-3; p4 and m4 and trigonid of m1 not shown. This specimen was previously referred to *Alphadon marshi* by Lillegraven (1969). Scale=1mm.



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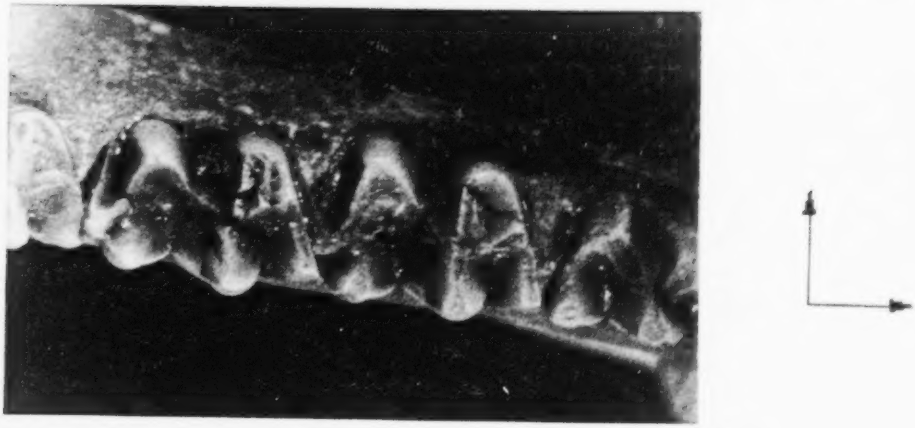
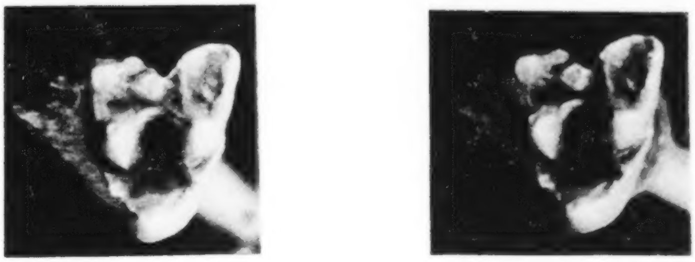


B

Plate 13. *Alphadon marshi*, Scollard Formation, Alberta. A) UALVP 2738, LM2; B) UALVP 2490, RM2; C) UALVP 2567, LM3; D) UALVP 2921, LM3. All specimens originally referred to "*Alphadon wilsoni*", all x13.



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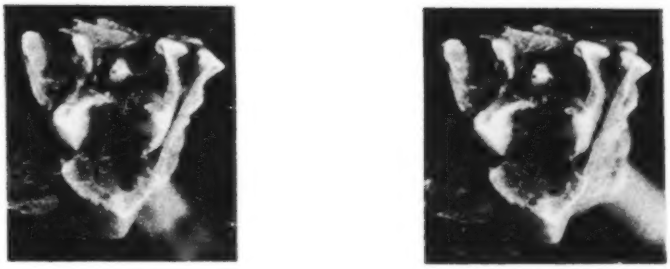

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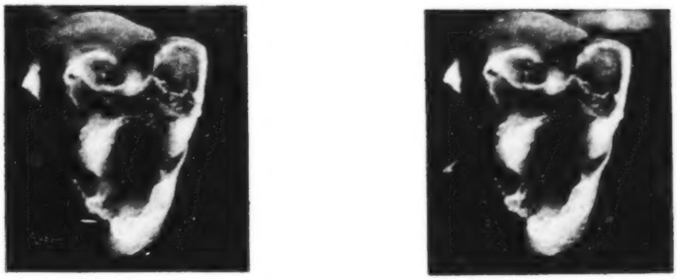

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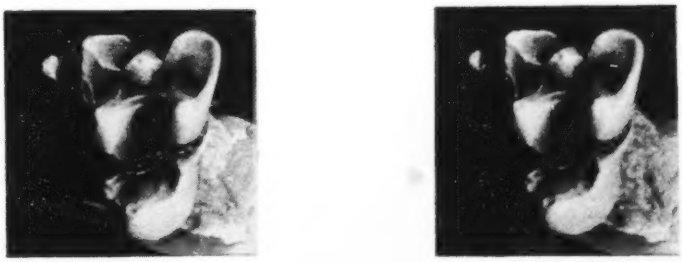

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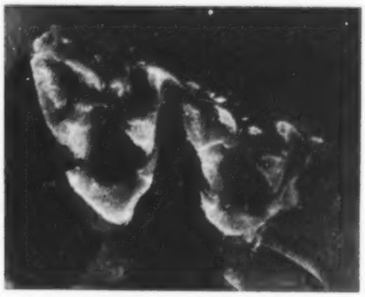
Plate 14. *Alphadon jasoni*, Scollard Formation, Alberta, Wounded Knee local fauna (Frenchman Formation), Saskatchewan. A) UCMP 51385, right maxillary fragment preserving M2-3; B) UALVP 2738, LM1; C) UALVP 22682, LM1; D) UALVP 22679, LM1; E) UALVP 2316, RM1; F) UALVP 22683, LM1; G) steropairs UALVP 22678, RM2; H) stereopairs UALVP 22678, LM2; I) UALVP 22685, RM2; J) UALVP 22687, RM2; K) UALVP 3740, LM2. All x11.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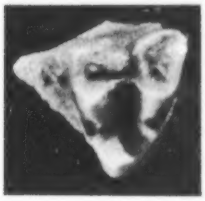
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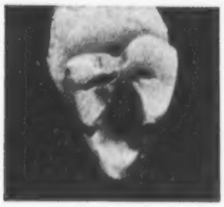
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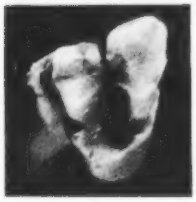
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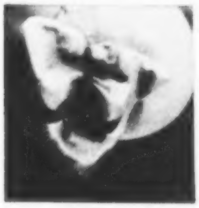
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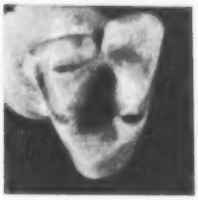
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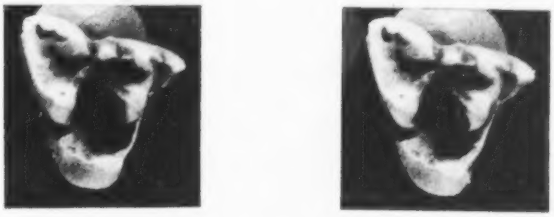
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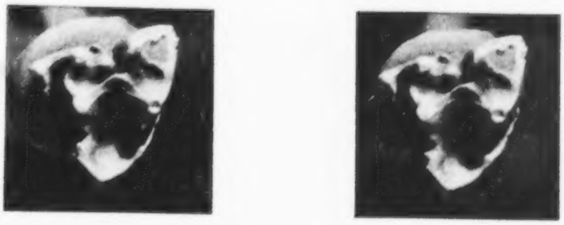
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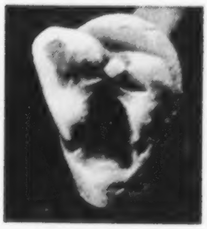
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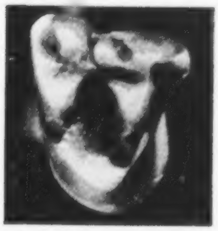
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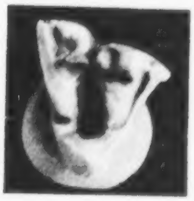
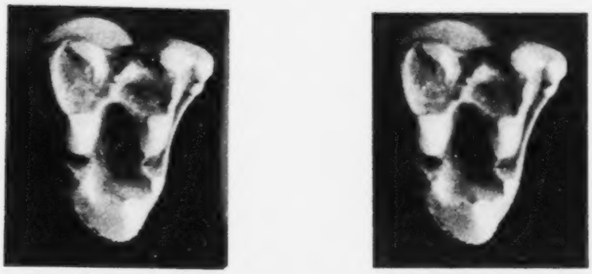

K

Plate 15. *Alphadon jasoni*, upper M3s, Scollard Formation, Alberta, Frenchman Formation, Saskatchewan. A) stereopairs, UALVP 22694, RM3; B) UALVP 3701, RM3; C) 22691, LM3; D) UALVP 22691, LM3; E) UALVP 22692, LM3. All x11.



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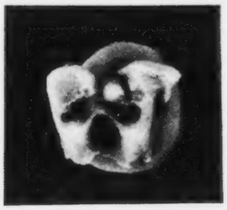

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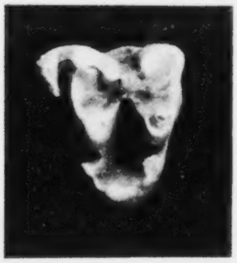

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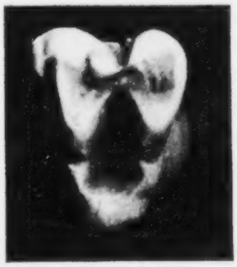
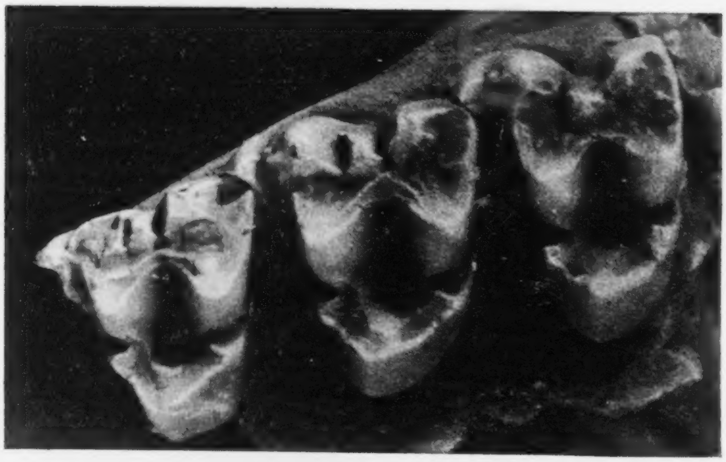


D

Plate 16. Morphological comparison of upper molars of *Alphadon marshi* and *Alphadon jasoni*. A) *Alphadon jasoni*, UALVP 2846, LM1-3; B) Holotype of *Alphadon marshi*, YPM 13659, RM3; (C) Holotype of "*Alphadon wilsoni*", UALVP 3146, RM2-3. All x13.



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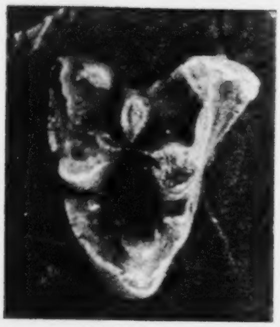

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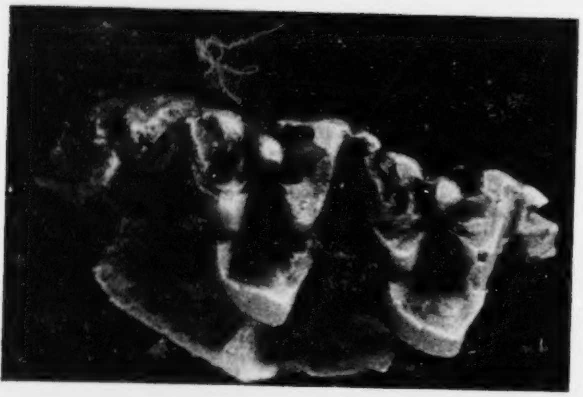
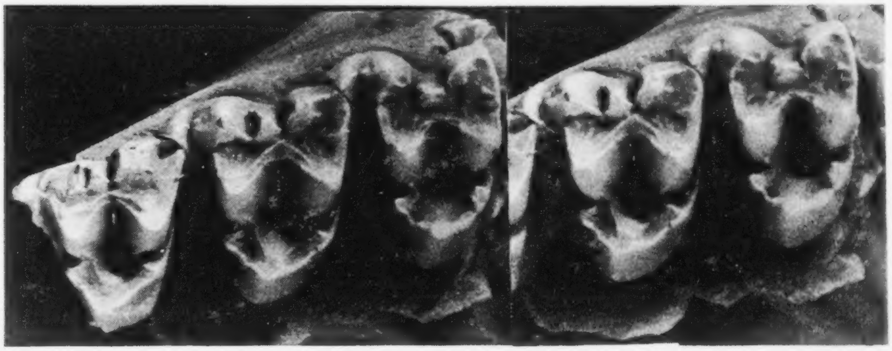


C

Plate 17. Morphological comparison of upper molars of *Alphadon marshi* and *Alphadon jasoni*, particularily in the degree of development of the centrocrista (dilambdodont upper molars). Steropairs, A) *Alphadon jasoni*, UALVP 2846, LM1-3 (LM1-2 observable in stereo only); B) Holotype of *Alphadon marshi*, YPM 13659, RM3; C) holotype of "*Alphadon wilsoni*", UALVP 3146, RM2-3. All x11.



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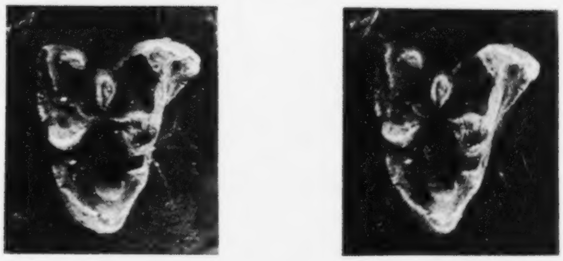

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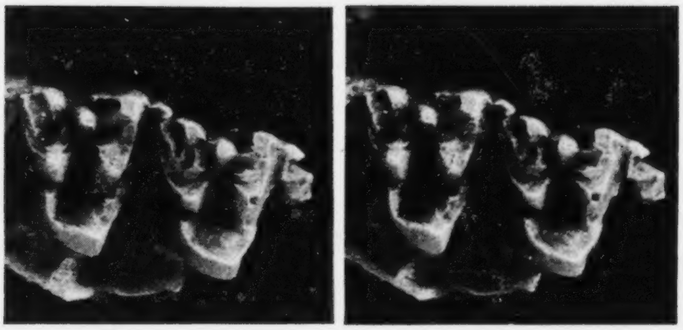
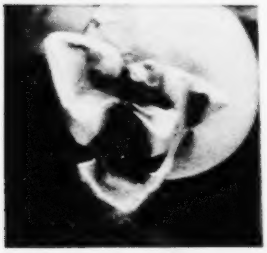


C

Plate 18. Size comparison of upper molars referred to *Alphadon jasoni*. Stereopairs, A) UALVP 2316 RM1, Scollard Formation, Alberta; B) UALVP 22678, RM2, Wounded Knee local fauna (Frenchman Formation), Saskatchewan; C) UALVP 2221, LM2, Scollard Formation, Alberta; D) UALVP 2758, LM2, Scollard Formation, Alberta. All x13.



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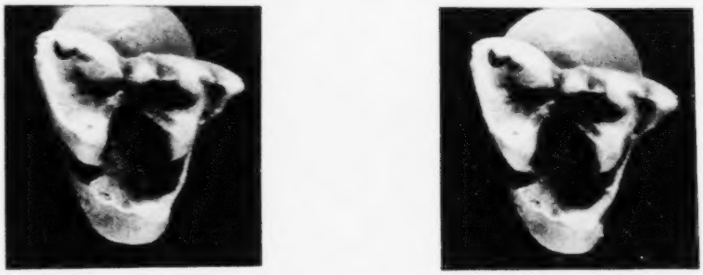

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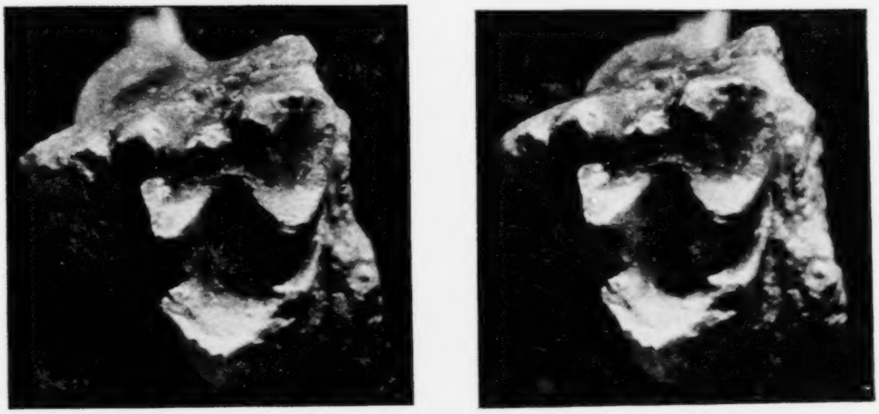
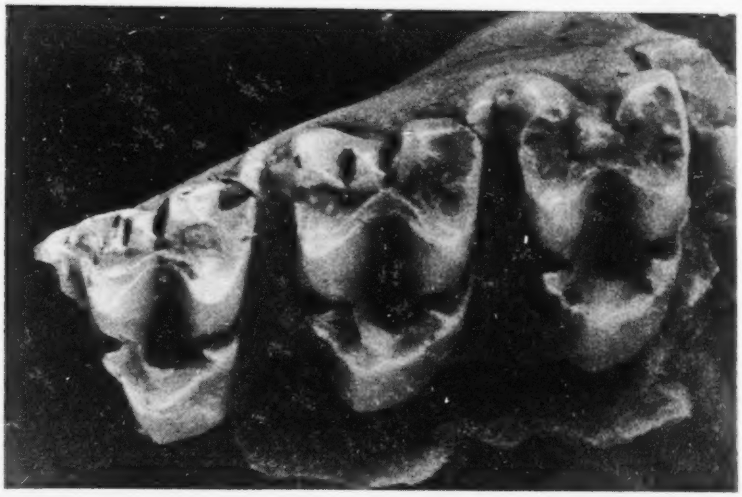


D

Plate 19. *Alphadon* sp., cf. *A. jasoni*, Scollard Formation, Alberta. A) UALVP 2846, includes upper (M1-4) and lower molars (p3-m4) found in occlusion. Shown are upper molars LM1-3; M4 not included in figure; B) UALVP 2758, LM2; C) UALVP 2454, LM2. All x13.



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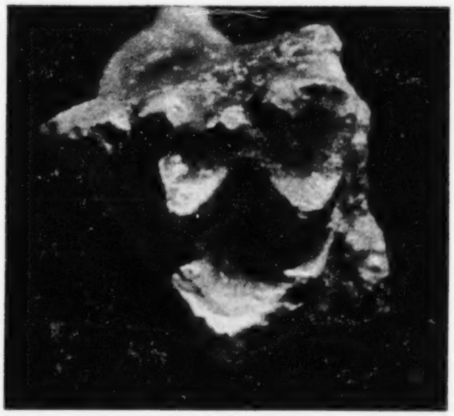

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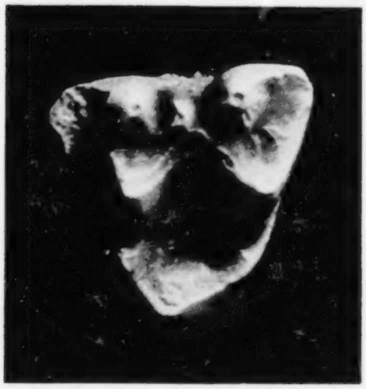
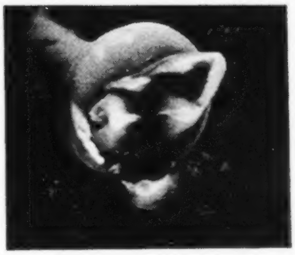
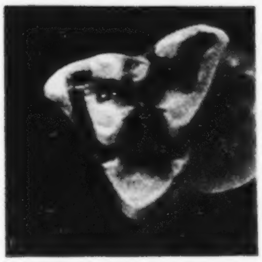


C

Plate 20. *Alphadon halleyi*. A) AMNH 77370, Judith River Formation, Montana, LM1; B) UALVP 6987, Oldman Formation, Alberta, LM1, both x 13; C) BNM-B1742, lowermost Kirtland Shale, New Mexico, camera lucida drawing, LM1; D) OMNH 20119, Kaiparowits Formation, Utah, camera lucida drawing, partial LM1; E) *Alphadon attaragos*, OMNH20147, Kaiparowits Formation, Utah, camera lucida drawing, LM1, scale = 1mm.



A



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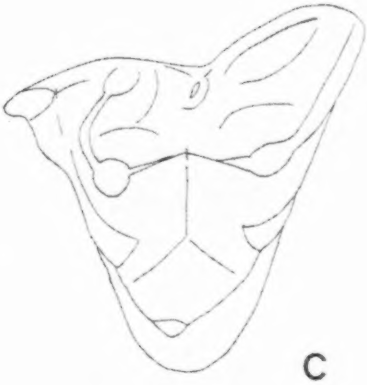

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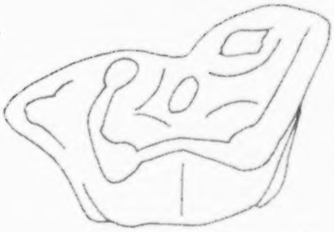

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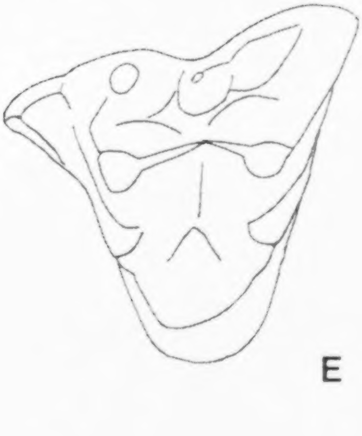

E

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APPENDIX 1: Student's t-test. A test of the significance of the difference (in terms of upper molar size) between the population means of larger (Scollard Formation specimens) and smaller specimens referred in this thesis to *Alphadon jasoni* on the basis of upper molar morphology.

Student's t- test: a test of the significance of the difference between two sample means

$$t_s = \frac{(\overline{Y}_1 - \overline{Y}_2) - (\mu_1 - \mu_2)}{\sqrt{\frac{(n_1 - 1)\, s_1^2 + (n_2 - 1)\, s_2^2}{n_1 + n_2 - 2} \left[\frac{n_1 + n_2}{n_1 n_2}\right]}}$$

where t_s is the sample statistic, $\overline{Y}_1$ and $\overline{Y}_2$ are the means of samples 1 and 2, μ_1 and μ_2 are the means of populations 1 and 2, s_1^2 and s_2^2 are the variances in samples 1 and 2, and n_1 and n_2 are the numbers of individuals of these samples.

degrees of freedom: $n_1 + n_2 - 2$

Students t- test: a test of the significance of the difference between two sample means

Scollard Formation upper molar specimens (M1s) referred to *A. jasoni* previously referred to *A. marshi*

$\bar{Y}_1 = 2.542$ mm $\qquad s_1^2 = .01$

$n_1 = 7$

Upper molar specimens (M1s) referred to *A. jasoni* from the Scollard (previously *A. wilsoni*), Frenchman and Lance Formations

$\bar{Y}_2 = 2.049$mm $\qquad s_2^2 = 0.02$

$n_2 = 19$

Testing the null hypothesis that the means of these two populations are equal-

$H_0: \mu_1 - \mu_2 = 0$

$H_1: \mu_1 - \mu_2 > 0$

degrees of freedom: 7+19-2 = 24

$$t_s = \frac{(2.542-2.049) - 0}{\sqrt{\frac{(7-1)(.01) + (19-1)(.02)}{7+19-2} \quad \frac{7+19}{133}}}$$

$$t_s = \frac{.493}{\sqrt{\frac{(.06)+(.36)}{24} \quad (.1954)}} = 8.428$$

the critical value of $t_{.05,[16]} = 1.746$ ($\alpha = .05$, one-tailed test). Since the value for t_s calculated above was 8.428 we must reject the null hypothesis above H_0: $\mu_1 - \mu_2 = 0$, and accept the alternate hypothesis that μ_1 (Scollard specimens previously referred to *A. marshi*), are significantly larger than others referred to *A. jasoni*.

Student's t- test: a test of the significance of the difference between two sample means

Scollard Formation upper molar specimens (M2s) referred to *A. jasoni* previously referred to *A. marshi*

$\bar{Y}_1 = 2.966\text{mm} \qquad s_1^2 = 0.002$

$n_1 = 4$

Upper molar specimens (M2s) referred to *A. jasoni* from the Scollard (previously *A. wilsoni*), Frenchman and Lance Formations

$\bar{Y}_2 = 2.137\text{mm} \qquad s_2^2 = 0.015$

$n_2 = 21$

Testing the null hypothesis that the means of these two populations are equal-

$$H_0 : \mu_1 - \mu_2 = 0$$

$$H_1 : \mu_1 - \mu_2 > 0$$

degrees of freedom: 4 + 21 - 2 = 23

$$t_s = \frac{(2.966-2.137) - 0}{\sqrt{\dfrac{(4-1)(.002) + (21-1)(.015)}{4+21-2}\left[\dfrac{4+21}{84}\right]}}$$

$$t_s = \frac{.829}{\sqrt{\dfrac{(.006)+(.3)}{23}\,[.298]}} = 13.174$$

the critical value of $t_{.05,[23]} = 1.714$ ($\alpha = .05$, one-tailed test). Since the value for t_s calculated above was 13.174, we must reject the null hypothesis above $H_0 : \mu_1 - \mu_2 = 0$, and accept the alternate hypothesis that μ_1 (represented by Scollard specimens previously referred to *A. marshi*), are significantly larger than others referred to *A. jasoni*.

Student's t- test: a test of the significance of the difference between two sample means

Scollard Formation upper molar specimens (M3s) referred to *A. jasoni* previously referred to *A. marshi*

$\bar{Y}_1 = 2.509\text{mm}$ $\quad s_1^2 = 0.032$

$n_1 = 2$

Upper molar specimens (M3s) referred to *A. jasoni* from the Scollard (previously *A. wilsoni*), Frenchman and Lance Formations

$\bar{Y}_2 = 2.189\text{mm}$ $\quad s_2^2 = 0.025$

$n_2 = 16$

Testing the null hypothesis that the means of these two populations are equal-

$$H_0 : \mu_1 - \mu_2 = 0$$

$$H_1 : \mu_1 - \mu_2 > 0$$

degrees of freedom: 2 + 16 - 2 = 16

$$t_s = \frac{(2.509-2.189)-0}{\sqrt{\dfrac{(2-1)(.032) \;+\; (16-1)(.025)}{2+16-2}\left[\dfrac{2+16}{32}\right]}}$$

$$t_s = \frac{.320}{\sqrt{\dfrac{(.032)+(.375)}{16}\,[.5625]}} = 2.675$$

the critical value of $t_{.05,[16]} = 1.746$ ($\alpha = .05$, one-tailed test). Since the value for t_s calculated above was 2.675, we must reject the null hypothesis above $H_0 : \mu_1 - \mu_2 = 0$, and accept the alternate hypothesis that μ_1 (represented by Scollard specimens previously referred to *A. marshi*), are significantly larger than others referred to *A. jasoni*.

APPENDIX 2: F-distribution: a test to determine whether the variance (in terms of upper molar size) in the population of *Alphadon jasoni* (including Scollard Formation specimens) is greater than that within a population of *Didelphis virginiana*.

F distribution: a comparison of two population variances

The F distribution is used here to determine whether the variance within the population of *Alphadon jasoni* measured is equal to or greater than variance within a population of *Didelphis.* This comparison is based on the variance in two samples of these populations.

$$F = \frac{s_1^2}{s_2^2}$$

where F is the sample statistic, s_1^2 and s_2^2 are the sample variances of *Alphadon jasoni* and *Didelphis virginiana.*

degrees of freedom: v_1, v_2,= n_1-1

F distribution: a comparison of two population variances

Upper molar specimens (M1s) referred to *Didelphis virginiana*

$s_1^2 = 0.079$
$n_1 = 55$

Upper molar specimens (M1s) referred to *Alphadon jasoni*

$s_2^2 = 0.072$
$n_2 = 27$

Testing the null hypothesis that the variances of the two populations represented by *Alphadon jasoni* and *Didelphis virginiana* are equal-

$H_0: \sigma_1^2 = \sigma_2^2$
$H_1: \sigma_1^2 < \sigma_2^2$

the null hypothesis suggests that the variation in *Didelphis virginana* is equal to that seen in *Alphadon jasoni*; therefore, *A. jasoni* should not be split into two species on the basis of size. The alternative hypothesis suggests that the variation in *Didelphis virginana* is less than that seen in *A. jasoni* (i.e., the variance within *A. jasoni* is greater) and *A. jasoni* should be divided into two species.

degrees of freedom: v1= 55-1= 54; v2= 27-1= 26

$$F = \frac{0.079}{0.072}$$

$$F = 1.097$$

the critical value of $F_{[v1=54;\ v2=26]}$ is between 1.85 and 1.80 (=.05 one-tailed test). Since the value for F calculated above was 1.097, we cannot reject the null hypothesis, that the population variances are equal.

F distribution: a comparison of two population variances

Upper molar specimens (M2s) referred to *Didelphis virginiana*

$s_1^2 = 0.121$
$n_1 = 58$

Upper molar specimens (M2s) referred to *Alphadon jasoni*

$s_2^2 = 0.109$
$n_2 = 25$

Testing the null hypothesis that the variances of the two populations represented by *Alphadon jasoni* and *Didelphis virginiana* are equal-

$H_0 : \sigma_1^2 = \sigma_2^2$
$H_1 : \sigma_1^2 < \sigma_2^2$

the null hypothesis suggests that the variation in *Didelphis virginana* is equal to that seen in *Alphadon jasoni*; therefore, *A. jasoni* should not be split into two species on the basis of size. The alternative hypothesis suggests that the variation in *Didelphis virginana* is less than that seen in *A. jasoni* (i.e., the variance within *A. jasoni* is greater) and *A. jasoni* should be divided into two species.

degrees of freedom: v1= 58-1= 57; v2= 25-1= 24

$$F = \frac{0.121}{0.109}$$

$$F = 1.110$$

the critical value of F [v1= 57; v2= 24] is between 1.89 and 1.84 (=.05 one-tailed test). Since the value for F calculated above was 1.110, we cannot reject the null hypothesis, that the population variances are equal.

F distribution: a comparison of two population variances

Upper molar specimens (M3s) referred to *Didelphis virginiana*

$s_1^2 = 0.148$

$n_1 = 55$

Upper molar specimens (M3s) referred to *Alphadon jasoni*

$s_2^2 = 0.034$

$n_2 = 18$

Testing the null hypothesis that the variances of the two populations represented by *Alphadon jasoni* and *Didelphis virginiana* are equal-

$H_0: \sigma_1^2 = \sigma_2^2$

$H_1: \sigma_1^2 < \sigma_2^2$

the null hypothesis suggests that the variation in *Didelphis virginana* is equal to that seen in *Alphadon jasoni*; therefore, *A. jasoni* should not be split into two species on the basis of size. The alternative hypothesis suggests that the variation in *Didelphis virginana* is less than that seen in *A. jasoni* (i.e., the variance within *A. jasoni* is greater) and *A. jasoni* should be divided into two species.

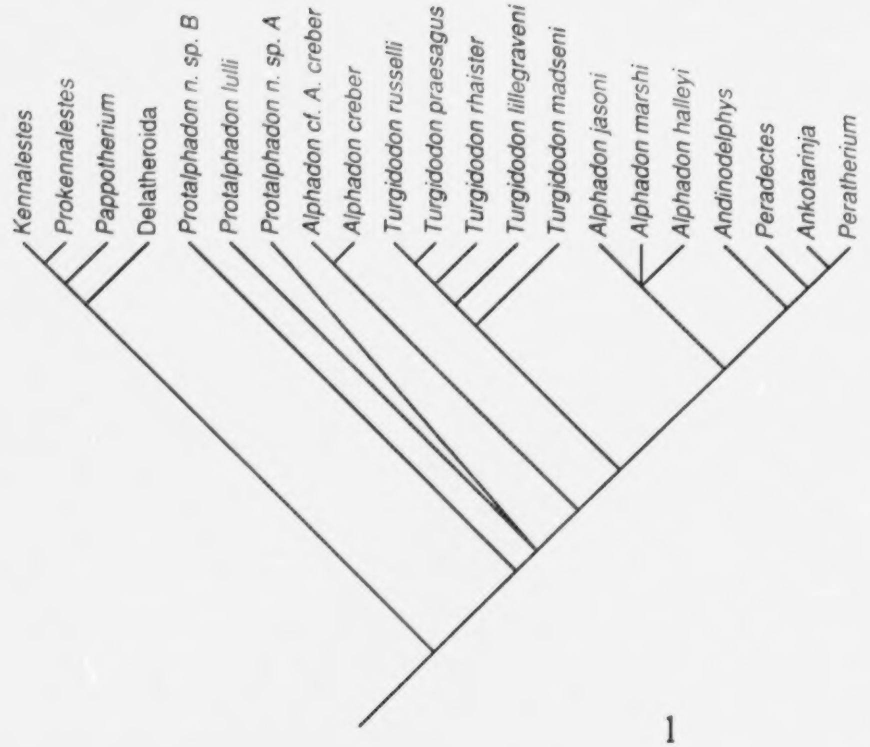
degrees of freedom: v1= 55-1= 54; v2= 18-1= 17

$$F = \frac{0.148}{0.034}$$

$$F = 4.35$$

the critical value of F [v1= 54; v2= 17] is between 2.92 and 2.83 (= .05 one-tailed test). Since the value for F calculated above was 4.35, we can reject the null hypothesis, that the population variances are equal.

APPENDIX 3: 36 minimal length trees (length 638, C. I., .663) produced by the branch and bound methodology (PAUP 3.0) from the data set in which characters 16 and 39 were ordered and all characters reweighted (Farris, 1969).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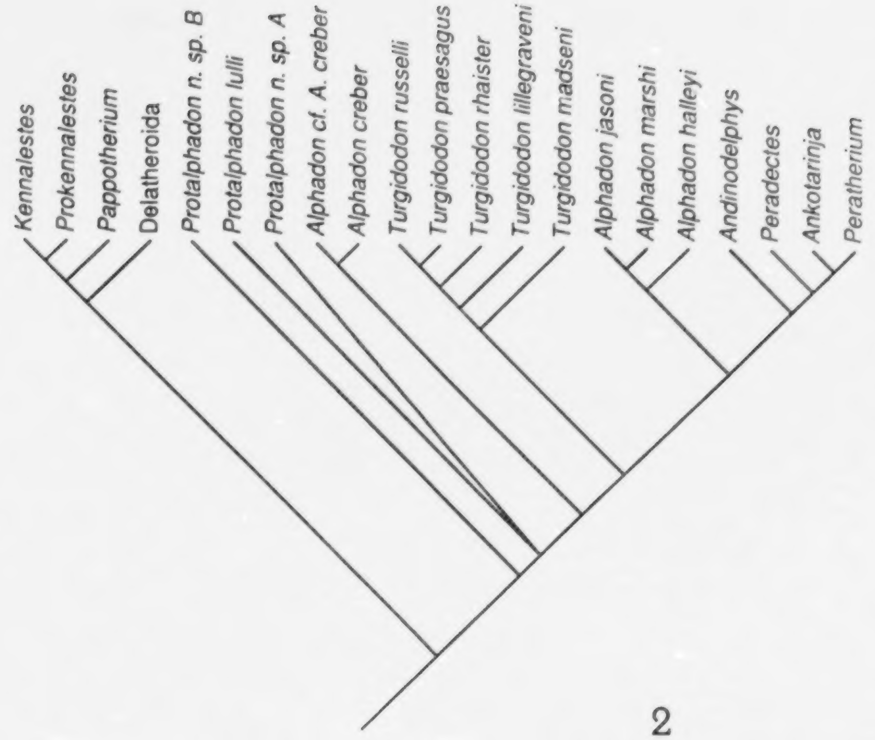
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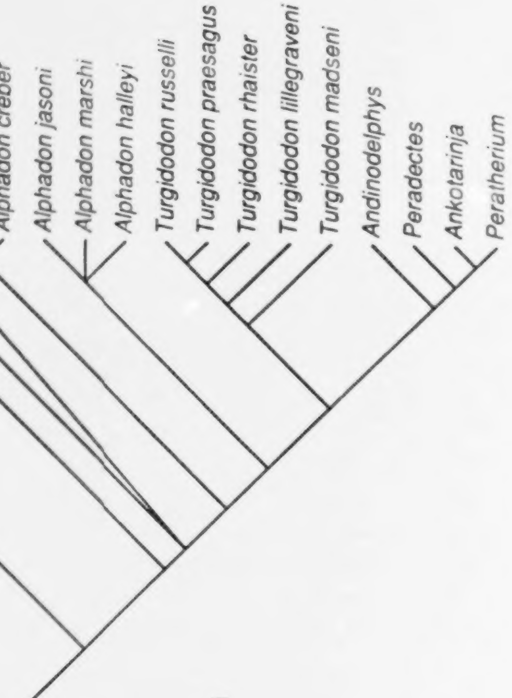
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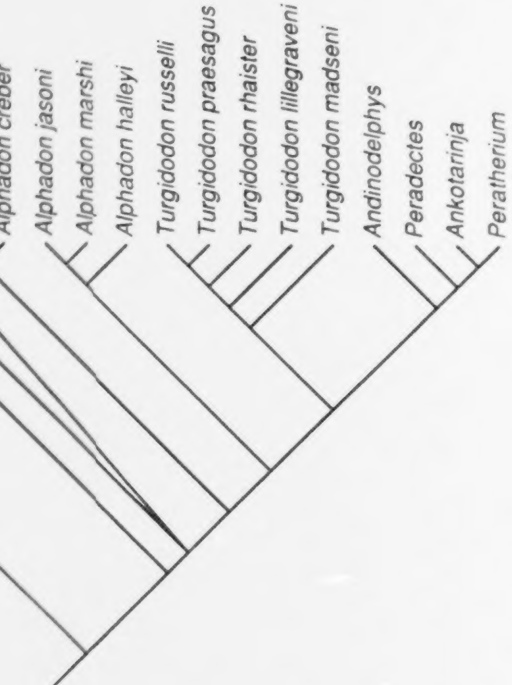
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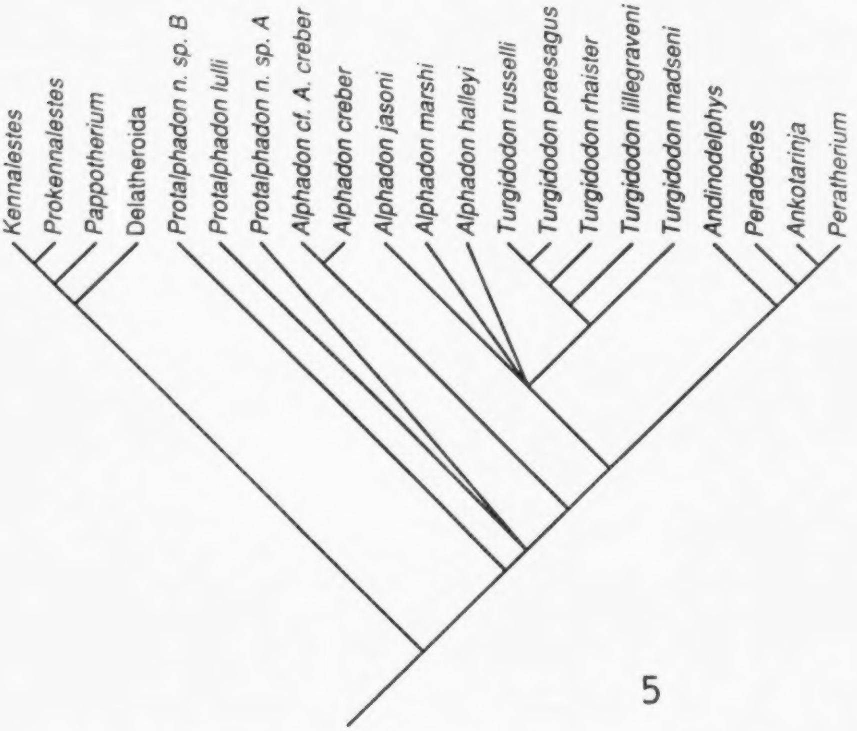
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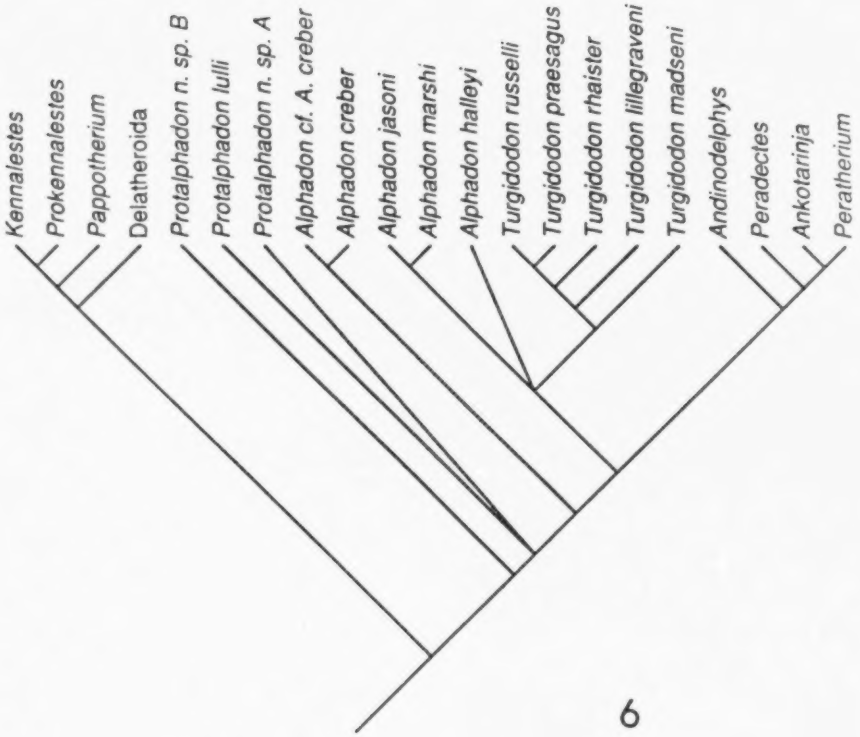
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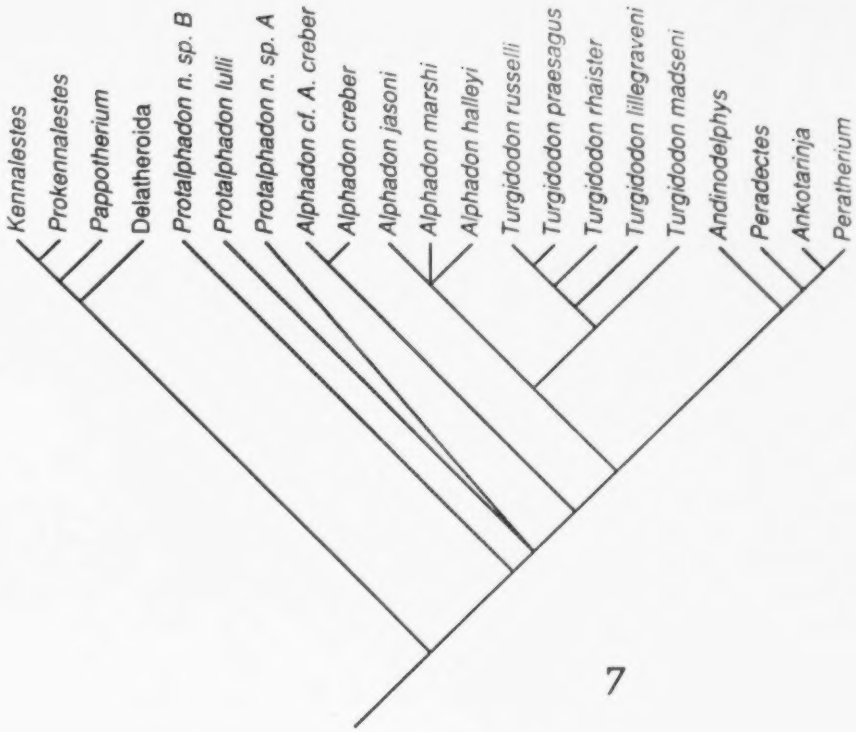
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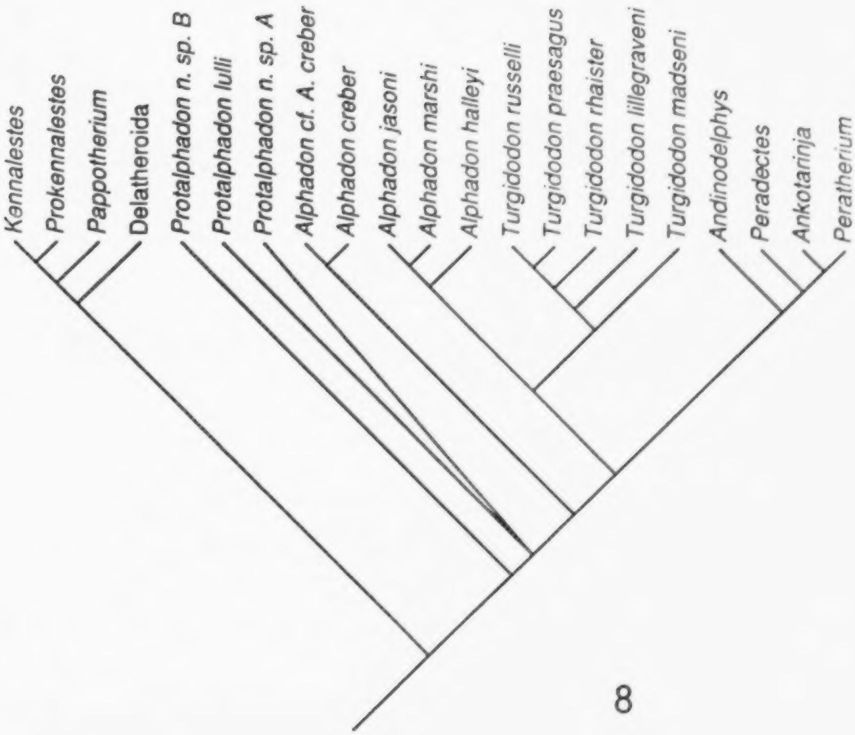
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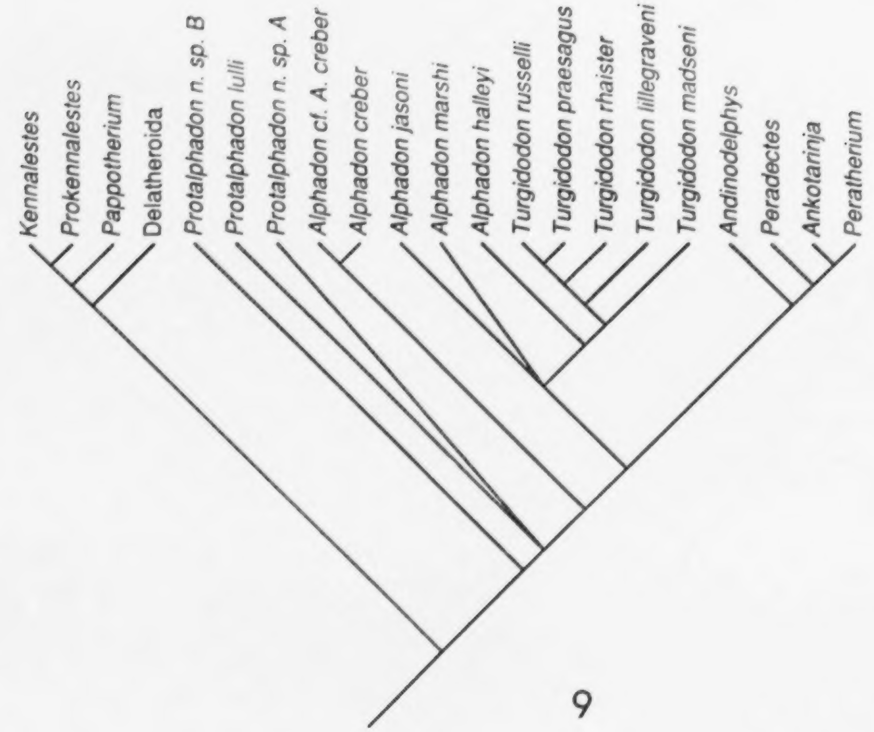
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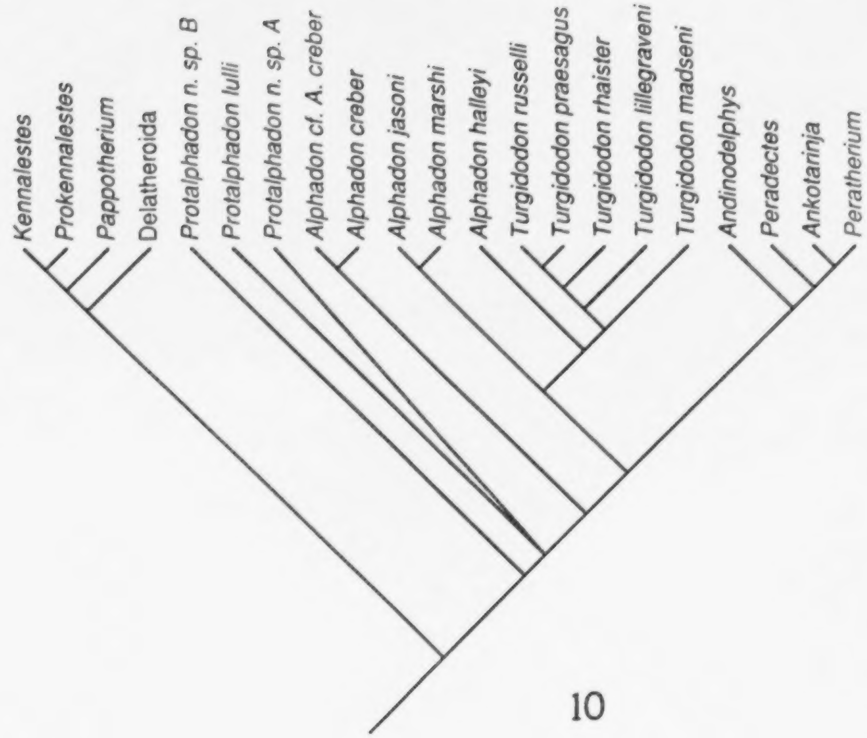
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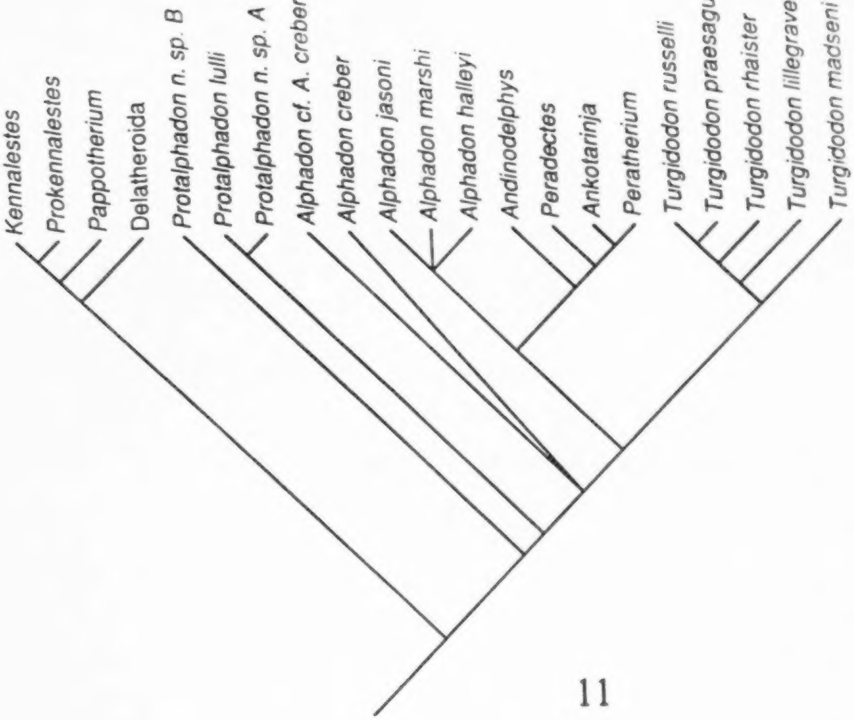
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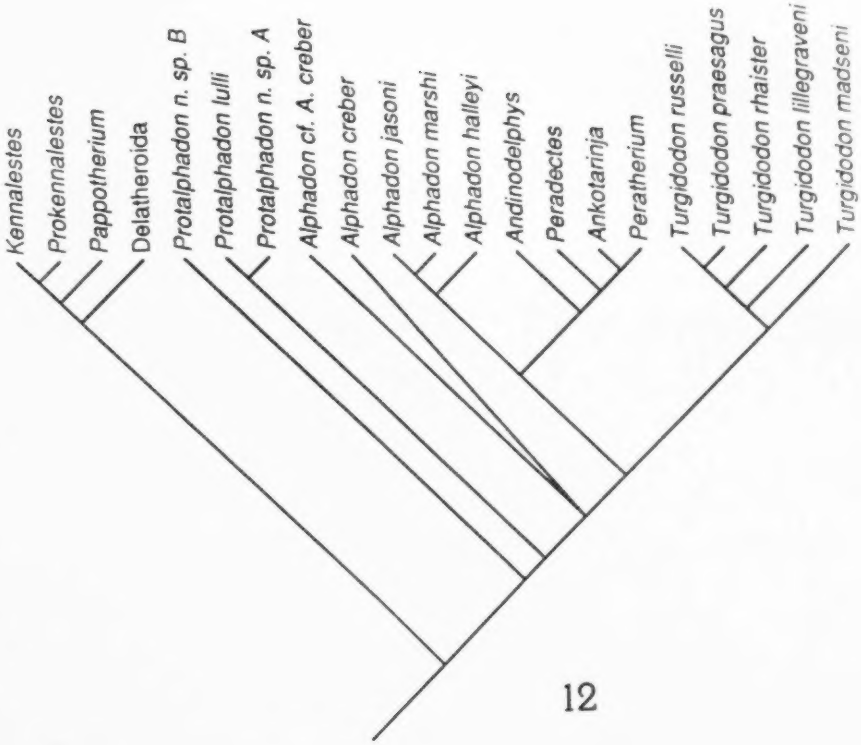
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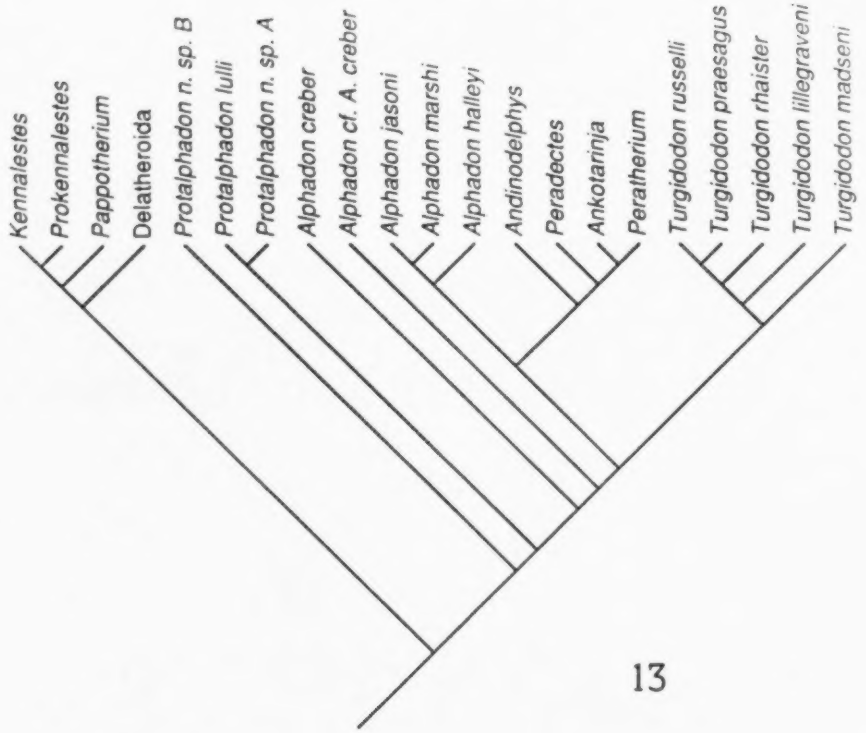
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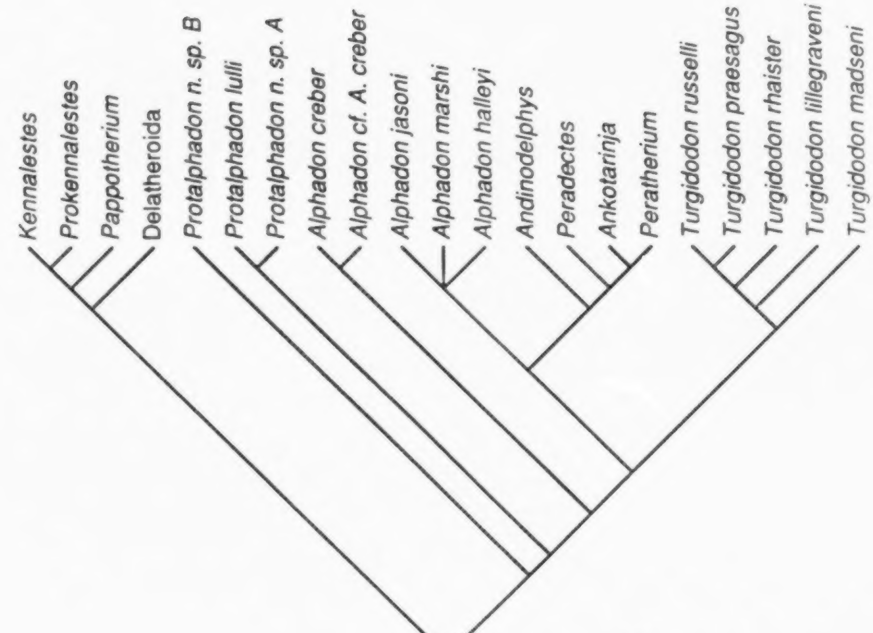
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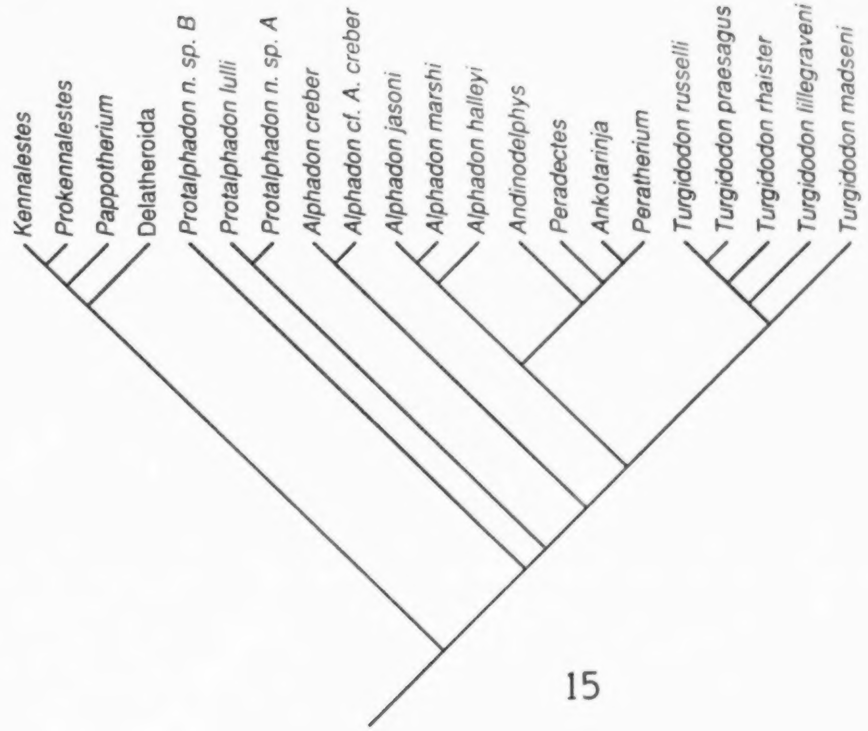
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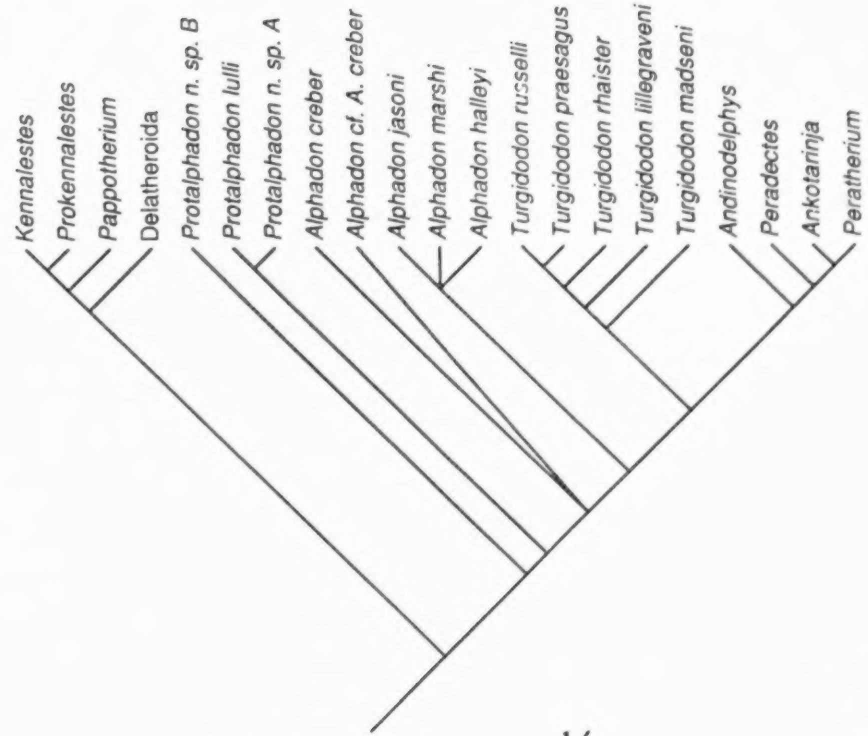
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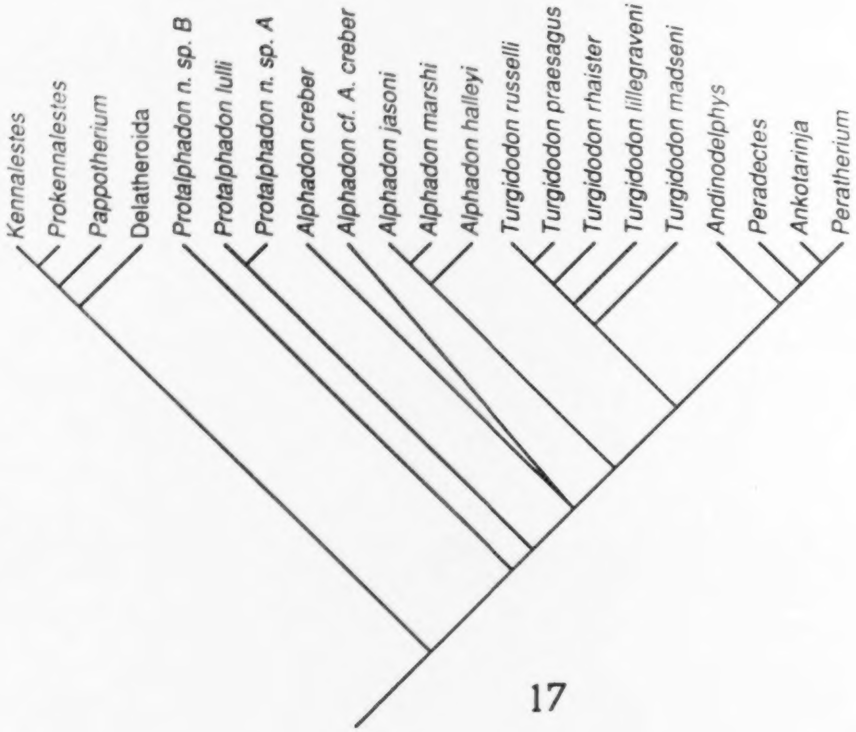
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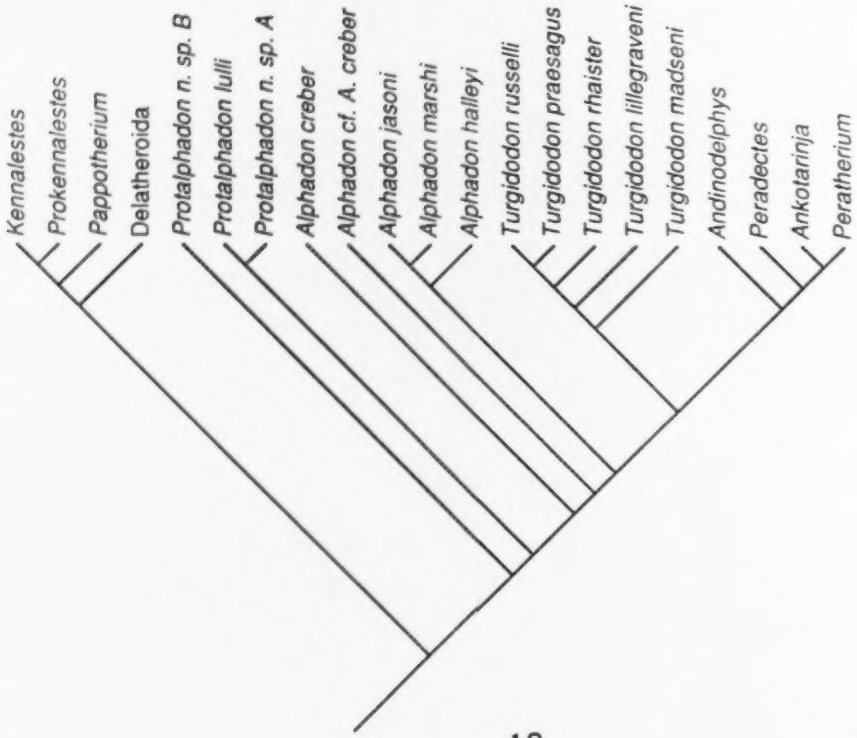
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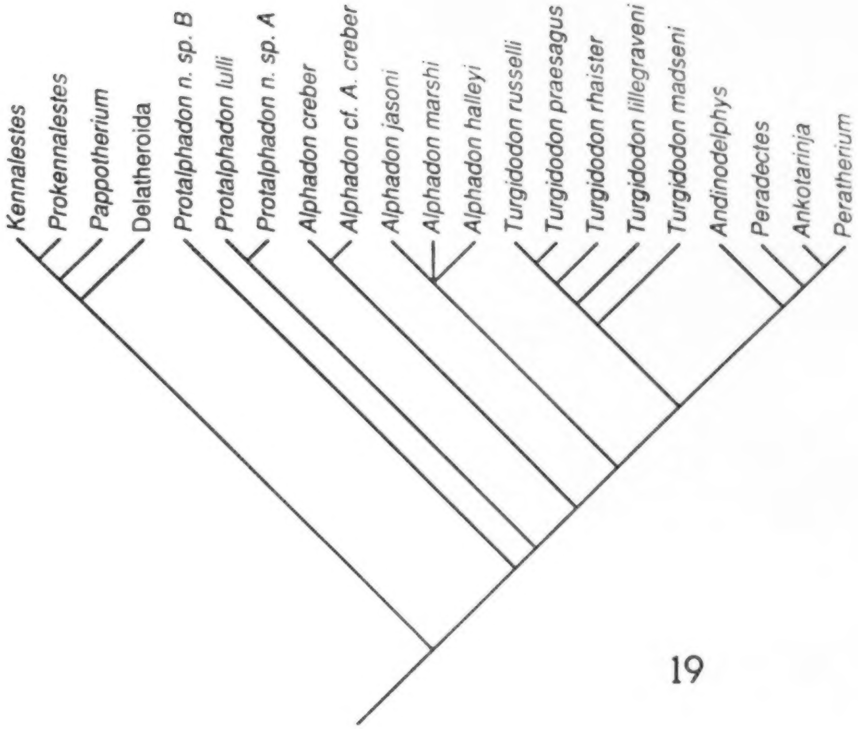
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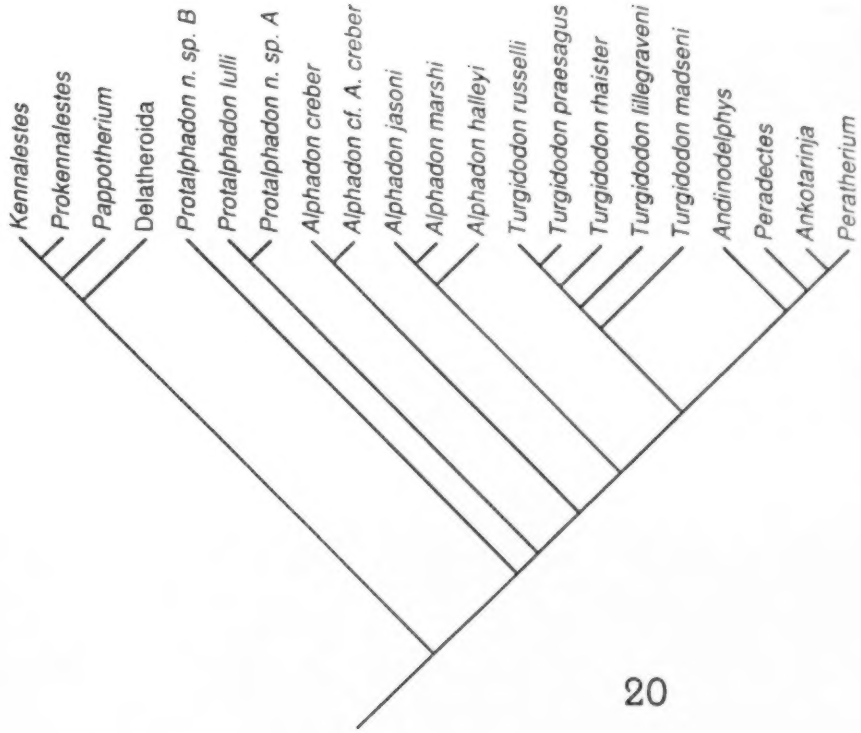
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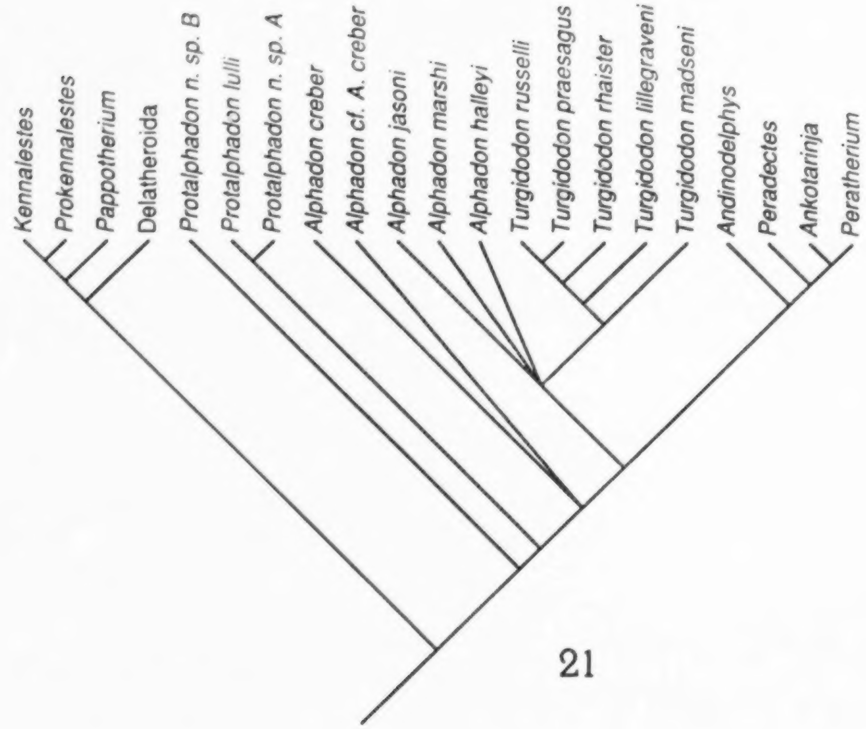
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Peratherium

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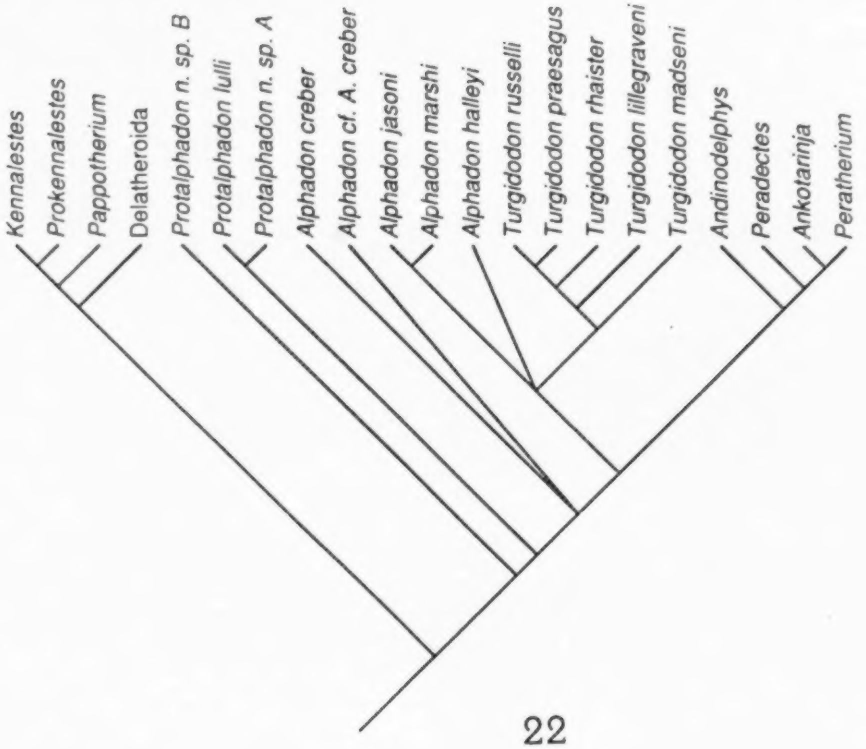
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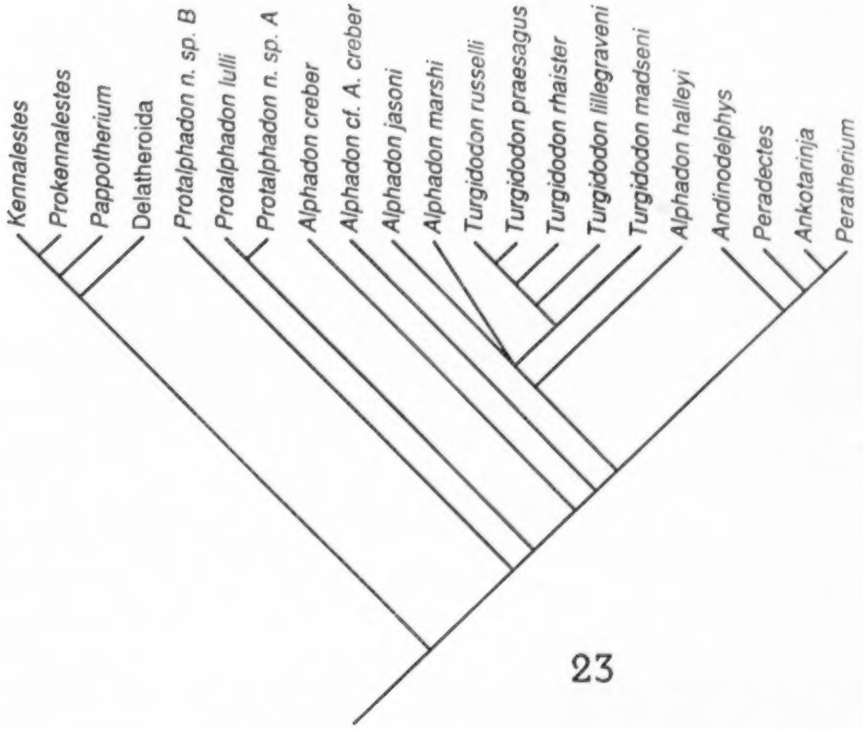
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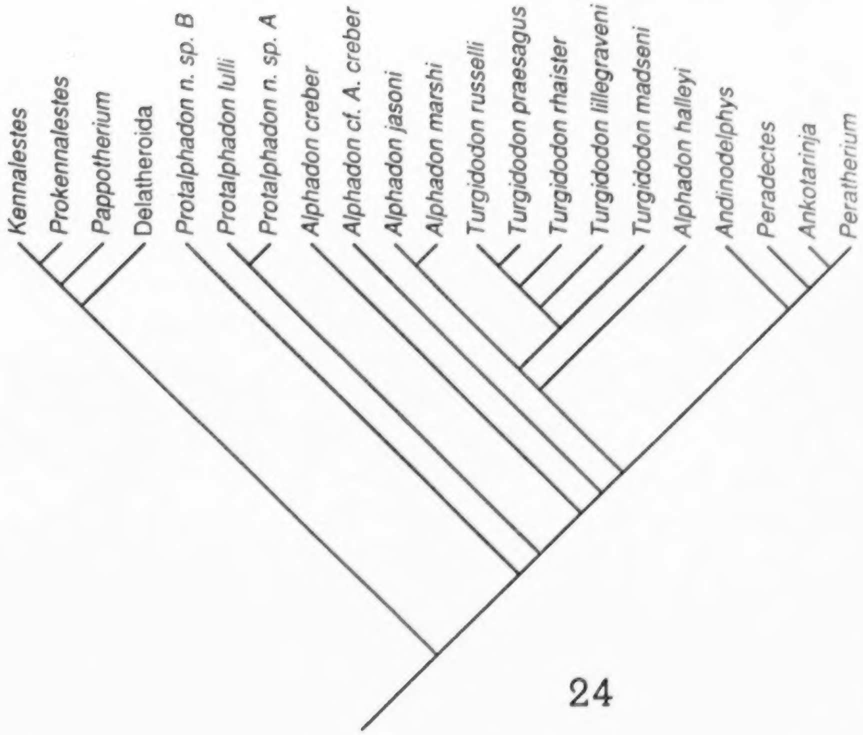
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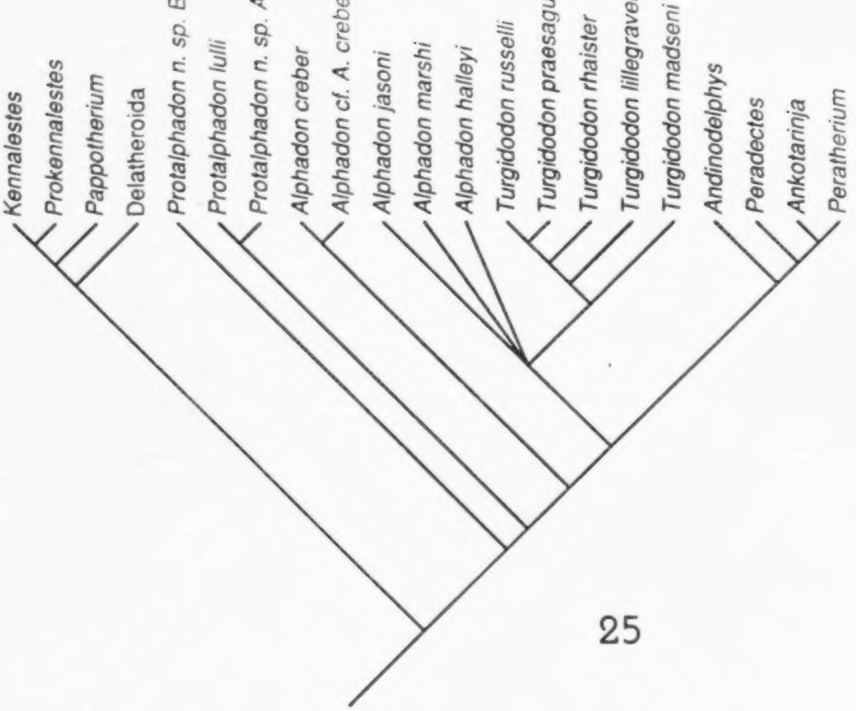
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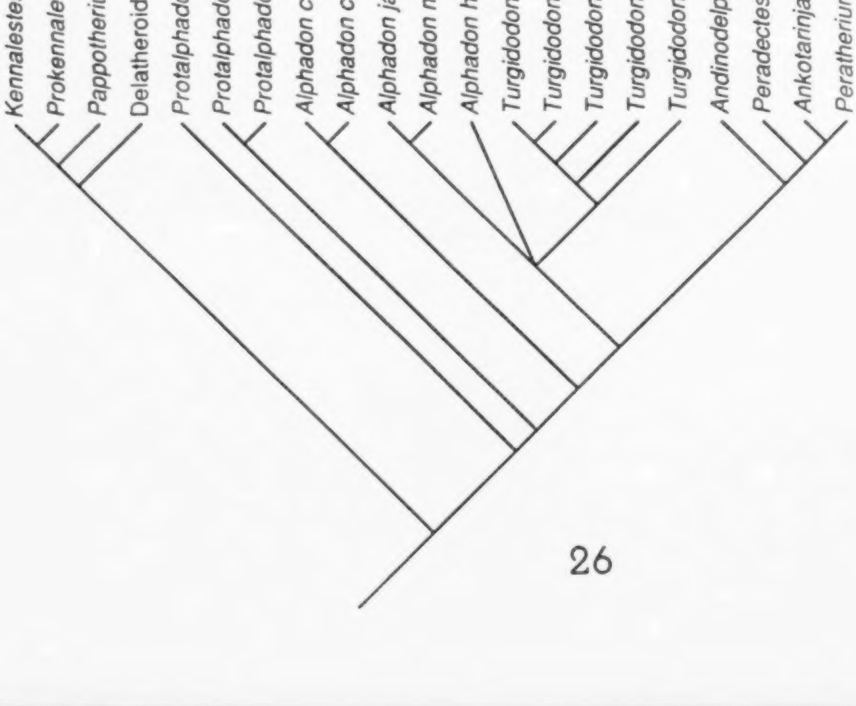
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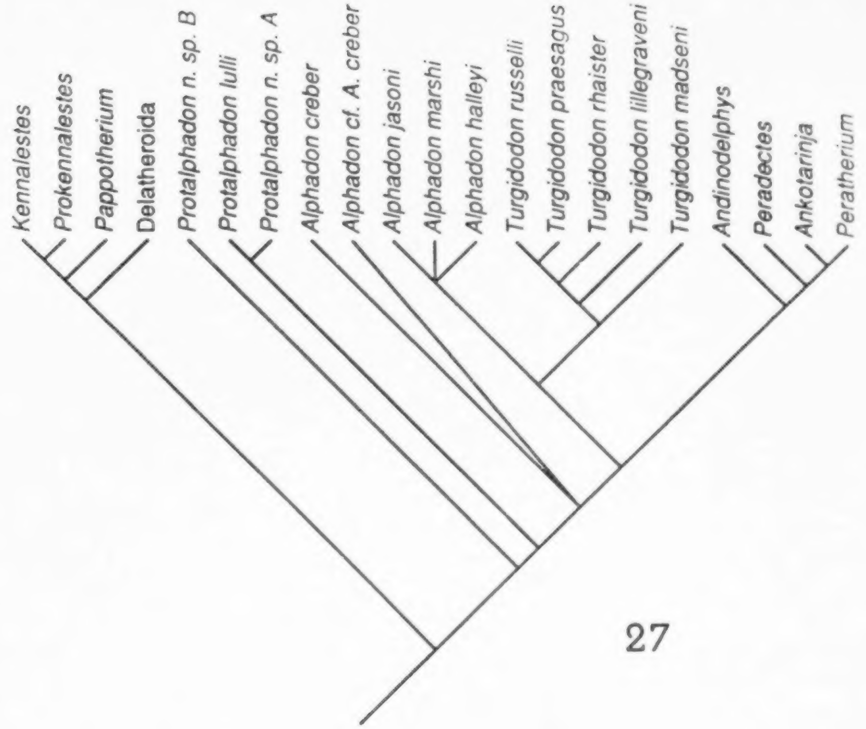
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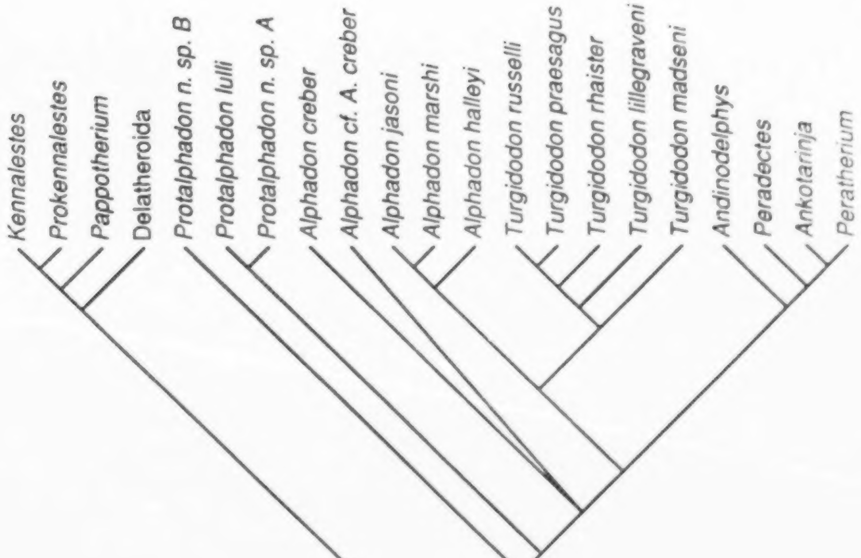
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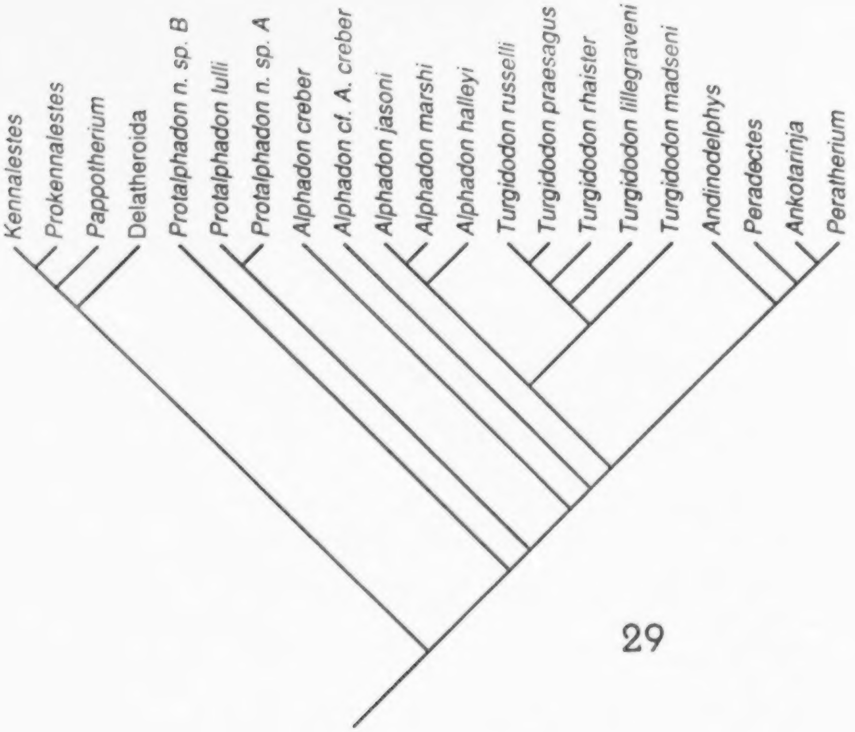
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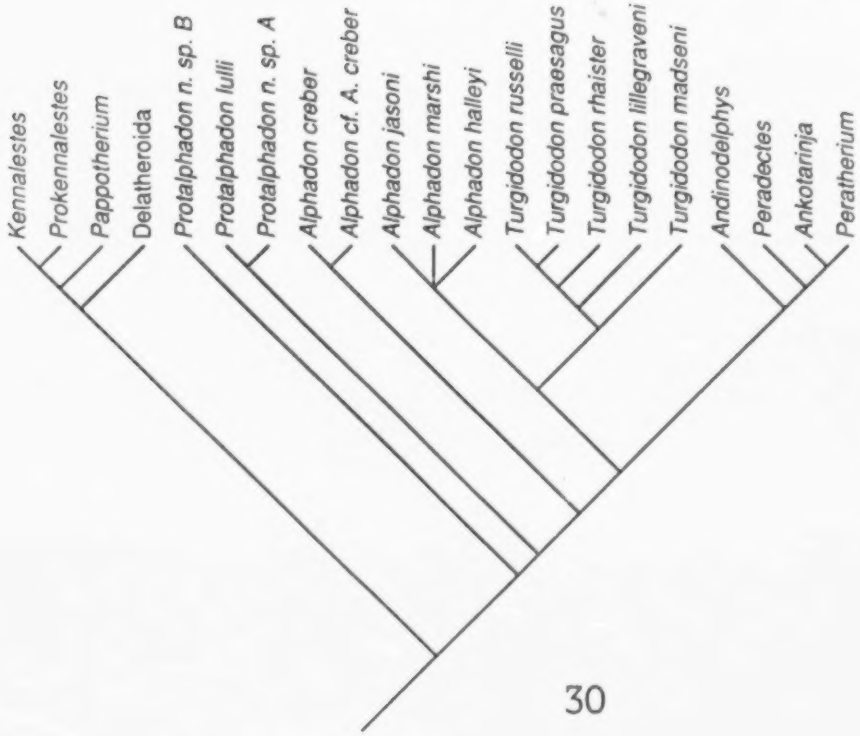
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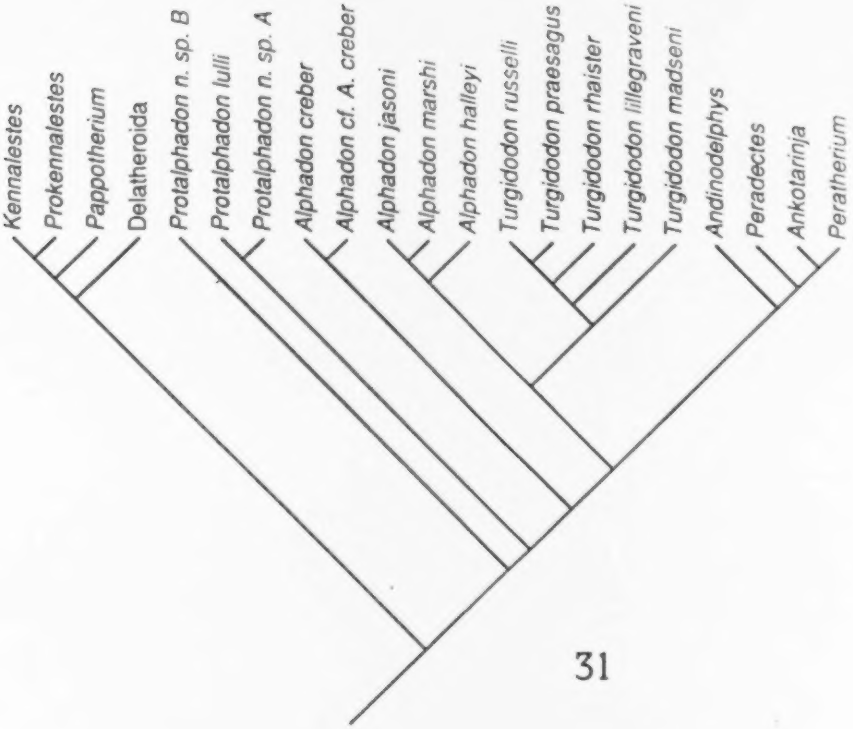
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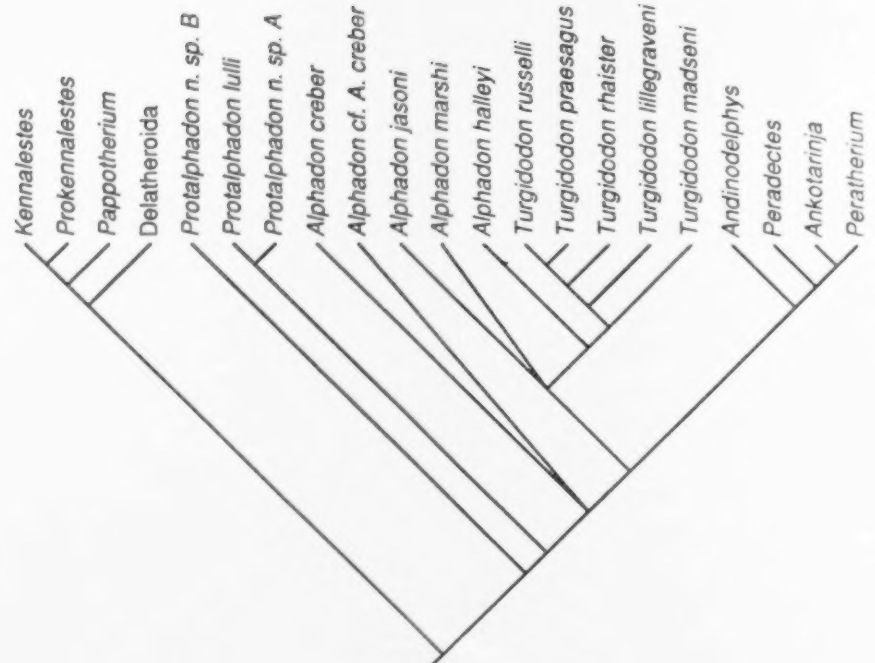
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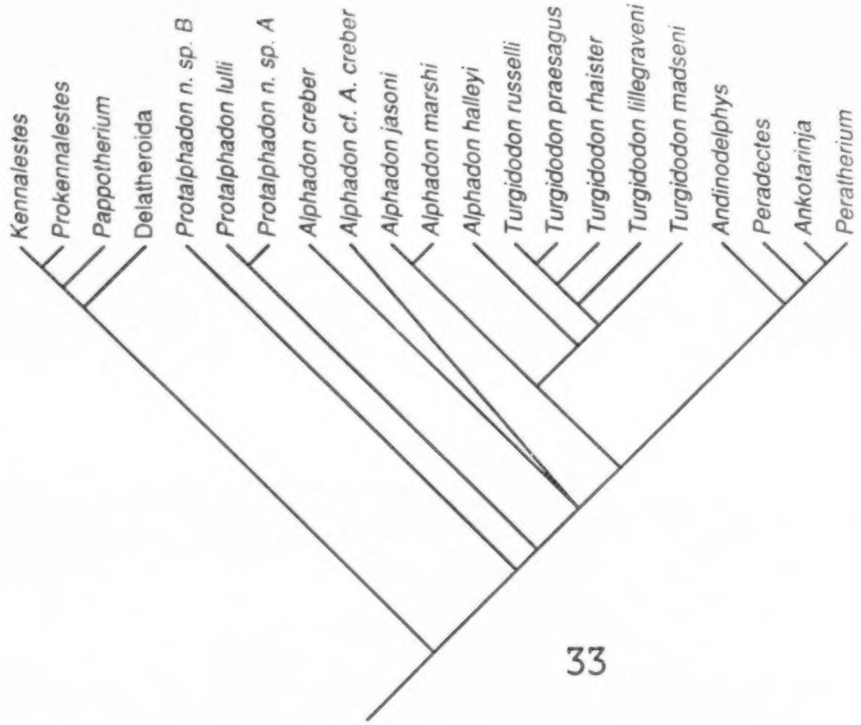
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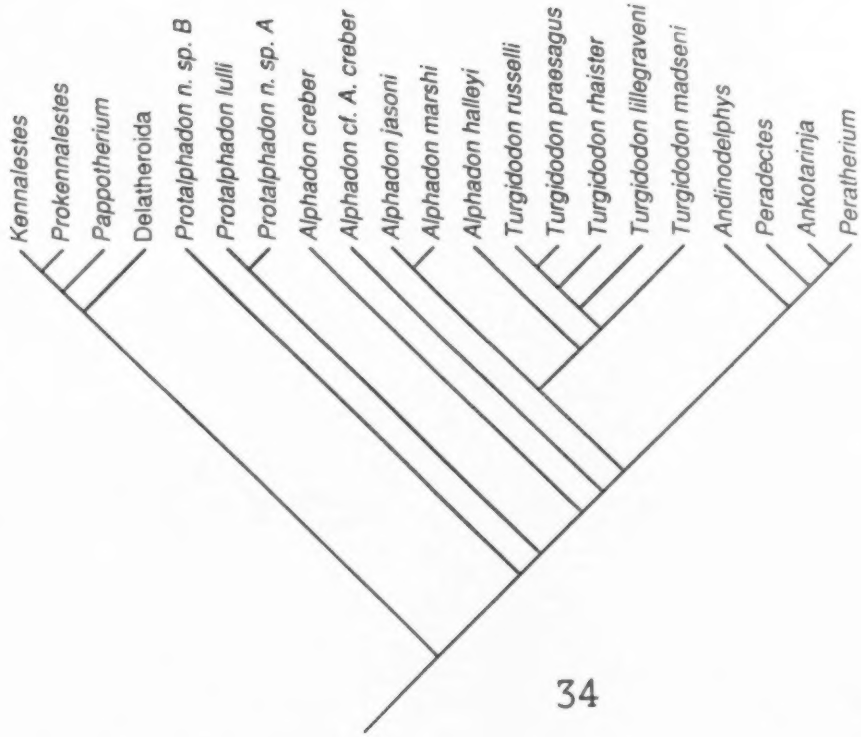
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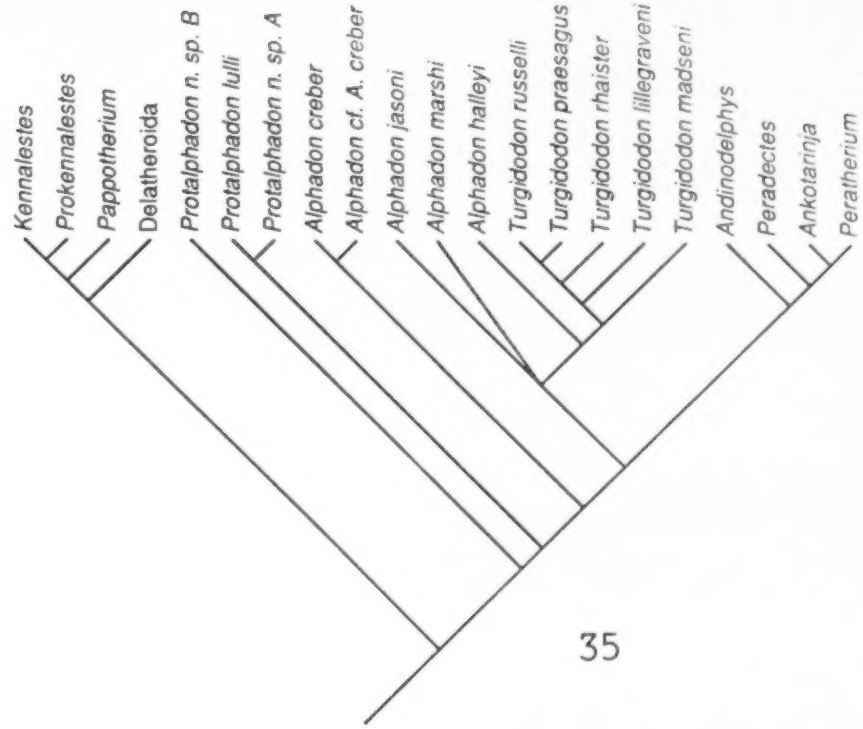
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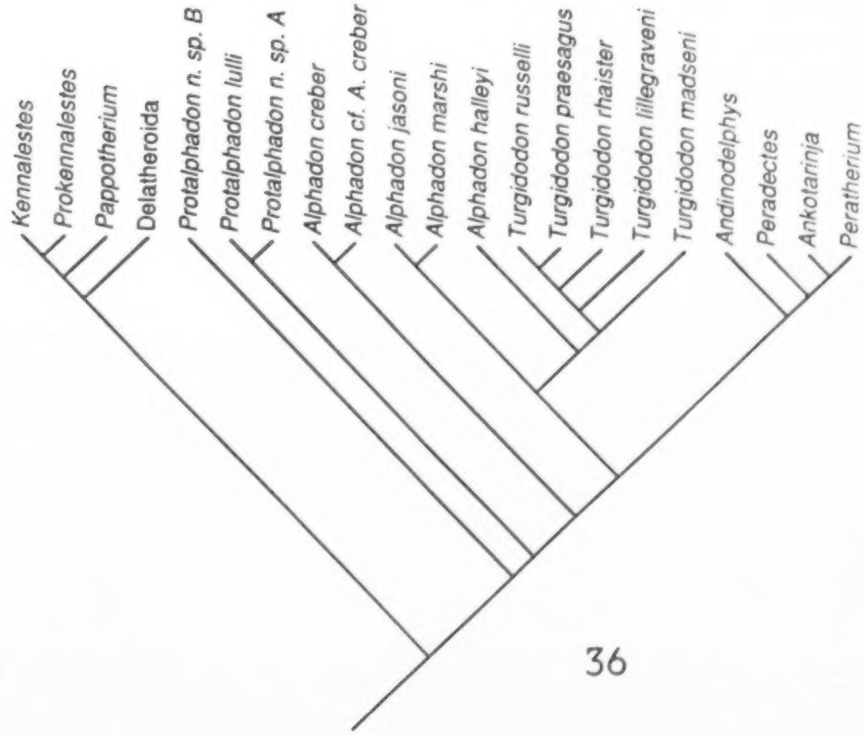
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